Spatial ecology and conservation of the critically endangered swift parrot

By

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CANDIDATE'S DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Matthew H. Webb Date: 21/9/2017

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ABSTRACT

Conservation of highly mobile resource specialists depends on understanding where and when resources are available and how populations respond to resource configuration. These species are often resource specialists, which can make them vulnerable to resource bottlenecks in time and space. When they also have dynamic distributions, data collection and conservation planning is extremely challenging. Therefore, for species like the swift parrot, which is a highly mobile resource specialist with a dynamic distribution, ecologically relevant and spatiotemporally explicit estimates of distributions are urgently needed to guide conservation planning.

Prior to this research little was known of spatiotemporal variation in the distribution of the critically endangered migratory swift parrot in its breeding range. The swift parrot requires co-occurrence of two key functional habitats to breed (nesting and foraging) and relies on the flowering of *Eucalyptus globulus and E. ovata* for food. The overall aim of this research was to better understand and quantify the spatial ecology of the species to improve conservation planning and outcomes. The main impetus for this research was continuing extensive habitat loss (as a result of industrial-scale logging and land clearance) without an understanding of i) the importance of the loss of key sites or locations and ii) the implications of the discovery of novel predator during the course of the study.

Firstly, this thesis quantifies and describes a key functional habitat feature (i.e. nesting trees) to assist accurate identification of nesting habitat **(Chapter 2)**. The research then uses data from a unique multi-year monitoring program to i) extend modelling

approaches to account for imperfect detection and spatial autocorrelation, ii) quantify the strong link between changing food availability and the species distribution, and iii) quantify how this varies over time **(Chapter 3)**. Then, using data sampled from each functional habitat the research quantifies annual change in the use, location and availability of functional habitats over the entire breeding range **(Chapter 4)**. Finally, the abundance-occupancy relationship (AOR) is quantified temporally and spatially to better understand the implications of spatiotemporal changes in abundance and resource availability for the interpretation species distribution models (SDMs) **(Chapter 5)**.

This research reveals highly aggregated nesting behaviour of the swift parrot at multiple spatial scales, and provides one of the first macroecological examples to quantify a direct link between the spatiotemporal distribution of a highly mobile species and food availability. This spatiotemporal variation in food not only means the availability of functional habitats can vary dramatically between years, but also that an increase or decrease in one functional habitat does necessarily correspond to a relative increase or decrease in the other. This has important ramifications for interpreting SDMs, identifying when and where resource bottlenecks may occur, and the assessment of exposure to other spatially variable threats (e.g. predation). Further, the research shows the AOR for mobile species in dynamic distributions can be highly variable over time and space.

Importantly, the results also highlight that locations with high predicted occupancy and/or abundance do not necessarily equate to areas of high quality habitat. This thesis delivers some of the first fundamental and quantitative insights into the spatial ecology of highly mobile species that rely on variable environments, and provides guidance towards informing and developing conservation plans for this difficult to study group of species.

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DECLARATION OF AUTHOR CONTRIBUTIONS

Chapter 2

Authors (in order): Matthew H. Webb, Mark C. Holdsworth, and Janneke Webb

Author contribution: MHW designed the study, collected and analysed data, and wrote the manuscript. MCH and JW collected data and contributed to the manuscript.

Note: Glen McPherson Consultancy and Ross Cunningham kindly assisted with parts of the analyses.

Chapter 3

Authors (in order): Matthew H. Webb, Simon Wotherspoon, Dejan Stojanovic, Robert Heinsohn, Ross Cunningham, Phil Bell and Aleks Terauds

Author contribution: MHW conceived and designed the study, conceived and implemented analyses and wrote the manuscript. SW led the development of the GAM based occupancy modelling approach, (including the R code) and contributed to the manuscript. DS collected data and commented on the manuscript. RH and PB helped conceive the sampling design and contributed to the manuscript. RC assisted with early analyses and contributed to study design. AT worked with SW to develop the modelling approach, assisted with the analyses and contributed to the manuscript.

Chapter 4

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Author contribution: MHW conceived and designed the study, collected data, analysed data, implemented the occupancy models and wrote the manuscript. A. Terauds assisted with analyses, occupancy modelling and contributed to the manuscript. A. Tulloch implemented the MaxEnt modelling and contributed to the manuscript. DS collected data and commented on the manuscript. PB helped conceive the idea, collected data and commented on the manuscript. RH helped conceive the idea and commented on the manuscript.

Chapter 5

Authors (in order): Matthew H. Webb, Robert Heinsohn, William J. Sutherland, Dejan Stojanovic and Aleks Terauds

Author contribution: MHW conceived and designed the study, collected data, developed the models, and wrote the manuscript, RH and WJS helped conceive the study and contributed to the manuscript, DS collected data and contributed to the manuscript, AT developed the models, analysed data and contributed to the manuscript.

CHAPTER 1: INTRODUCTION

The world is experiencing a global extinction crisis, and anthropogenic change is recognised as the key driver (Barnosky et al. 2011). One of the frontiers in conservation biology is conserving highly mobile and migratory species that make large-scale movements between disparate locations to undertake different parts of their life cycle (eg. breeding) or in search of food resources (Runge et al. 2015). These large-scale movements present major challenges to conservation planning that are not typically posed by less mobile taxonomic groups.

Conservation planning for many migratory and nomadic species exemplifies the issues discussed above. Such planning is usually further compounded by chronic data deficiencies. Together, these issues often lead to ineffective conservation actions, ongoing population declines, or key knowledge gaps remaining unaddressed. Despite the well-known difficulties associated with studying many mobile species with large and dynamic distributions (Cottee-Jones et al. 2016), collecting new biological data is often essential for diagnosing *why* a species is declining, and determining the best management options (Canessa et al. 2015). However, for difficult to study species these challenges are often too easily dismissed as too difficult or not possible, while conservation resources continue to be directed towards specific actions without a clear understanding of a species' ecology and whether any positive benefit may result.

Nomadic migrants undergo large-scale irregular movement patterns, exhibiting plasticity in their geographic ranges over time (Newton 2006). Their movement strategies have

typically evolved to enable them to better track and exploit rich patches of sporadic and often spatially aggregated food. A major research challenge is to study them at ecologically relevant spatial and temporal scales (Dingle 2008) and robust empirical data on their movements are rare (Runge et al. 2014, 2015).

In this thesis I explore a variety of species distribution models to explore the spatiotemporal variation in range dynamics, changes in the availability of food, and subsequent effects on the availability of foraging and nesting habitat (hereafter: functional habitats) for a critically endangered nomadic migrant. I then examine how this affects the relation between abundance and occupancy.

Species distribution models (SDMs) are increasingly used to guide conservation planning by characterizing a species' ecological requirements and projecting this over unsampled areas (Guisan & Zimmerman 2000). The relative benefits of different modeling approaches have received considerable attention (Hastie & Fithian 2013; Guillera-Arroita et al. 2015). Models derived from systematically collected data on species' presences and absences perform better in terms of avoiding false positive and false negative errors than those based on less robust sampling designs (Guillera-Arroita et al. 2015). However, few nomadic migrants in dynamic environments have been studied using systematic sampling designs at ecologically relevant, large spatial scales (Runge et al. 2014). Hence limited data availability, especially the lack of absence records, can limit modeling approaches to less accurate presence-background techniques (Phillips et al. 2006).

Collecting detection/non-detection data from a sample of sites to be analysed within an occupancy-modelling framework is increasingly a popular approach to estimate species distributions (Kéry et al., 2013). Occupancy models and the relationship between occupancy and abundance, have been used extensively to estimate species density, distributions and habitat associations (e.g. Gaston et al., 2000; Hui et al., 2006). Estimating and accounting for false negative error rates or detection probability is fundamental to improving the reliability of occupancy models (MacKenzie et al., 2002; Martin et al., 2005; Royle and Nichols, 2003; Tyre et al., 2003; Wintle et al., 2004). The most common approach involves repeatedly sampling sites to estimate detection probability *p*, defined as the probability a species will be detected in a single site visit given that it occupies that site (MacKenzie et al., 2002). The detection process is commonly influenced by the behaviour and abundance of the target species (Gu and Swihart, 2004), and if there is spatial or temporal heterogeneity in *p*, establishing its relationships with environmental variables can reduce bias in parameter estimators and improve sampling strategies (e.g. Bailey et al., 2004; Gibson, 2011; Lahoz-Monfort et al., 2014).

Errors in interpreting ecological relationships can also arise if spatial autocorrelation (SAC) is ignored, or not accounted for in the distribution of the target species (Dormann, 2007; Hawkins, 2012; Legendre, 1993). Generally, SAC originates from either an autocorrelated environment (i.e. where nearby locations are more similar than more distant ones) or through processes like conspecific attraction and limited dispersal ability of the target species (Lichstein et al., 2002). Importantly, recognition and analysis of SAC can provide insights into ecological processes that may otherwise be overlooked (Bini et

al., 2009; Hawkins, 2012) and the effect of spatial structure has been recognised as an important component in modelling the occupancy-abundance relationship (Hui et al., 2006).

Another common limitation when modeling species distributions is that the resolution of spatial data layers used to predict a species' distribution may not reflect the resolution of the species' habitat use. Most SDMs are derived from macro-scale environmental characteristics (e.g. temperature, rainfall, vegetation cover) (Gaston and Fuller 2009) because continuous fine scale data on specific resources (e.g. food) are rarely available and often impractical to collect. If fine-scale habitat features determine species occurrence (i.e. functional habitats), a species' occupancy of the landscape is likely to be overestimated in SDMs that do not account for them (Gaston and Fuller 2009). For habitat specialists this effect is magnified because broad-scale environmental data rarely capture higher resolution heterogeneity of functional habitats (Jetz et al. 2008). Species also often require spatial and temporal co-occurrence of different resources (eg. food near nests - Brambilla and Saporetti 2014). Incorporating functional habitats into SDMs together with both presence and absence data is likely to improve model estimates and transferability of predictions to unsampled areas, but published examples are rare (eg. Vanreusel et al. 2007; Araújo and Luoto 2007).

Patterns of food availability in dynamic systems are often spatially autocorrelated, causing species to undergo dynamic changes in spatial aggregation (Kalle et al. 2018). For example, when resources are spatially widespread and dispersal and colonisation ability allows (Buckley and Freckleton, 2010), populations may expand their geographic range to exploit current conditions resulting in decreased spatial aggregation. Likewise,

when resources are scarce, high densities (or aggregations) of individuals may form. These patterns are not restricted to nomads, other species that rely on spatially dynamic food sources or have different movement strategies such as altitudinal or partial migrants also show plasticity in range dynamics (Boyle 2008; Sekercioglu 2010; Barçante et al. 2017; Bastille-Rousseau et al. 2017). Understanding these relationships for nomads might also provide insights into the range dynamics of these other species.

The effect of food availability may be further compounded if other resources are limited. For example, food is often the driver of animal movements, but if other required resources (e.g. nesting sites) are limited where food is abundant, this may have overall consequences for habitat quality or carrying capacity. In turn, this may result in changes in a species' distribution and density. Similarly, where nest sites are abundant, food limitation may constrain a species distribution or carrying capacity.

For highly mobile species like nomads, assuming local densities are a direct function of habitat suitability, resource availability or range size (eg. Brown et al. 1984; Holt et al. 1997) may be misleading and conflate the underlying ecological processes causing observed patterns (Boyle 2011). Similarly, the effects of dispersal ability and habitat patchiness that apply to less mobile species (Freckleton et al. 2005) are likely to be much weaker, or absent for nomads. The location and degree of aggregation of a species may make it more or less susceptible to non-habitat related threats (Buckley et al. 2017), resource bottlenecks and habitat loss (Runge et al. 2014). While high mobility may help nomads cope with changing environments (Kalle et al. 2018), resource availability and spatial variation in threats across their entire potential range needs to be considered in the context of their range dynamics.

These issues have important implications for the relationship between abundance and occupancy. The positive abundance-occupancy relationship (AOR) is a pervasive pattern in macroecology whereby species occupying more sites or with larger geographic distributions are generally more locally abundant. However, examples of AORs for highly nomadic species with variable distributions are extremely rare. In the AOR literature, temporal trends (i.e. temporal AORs) have also received less attention than inter-specific or spatial forms of AOR (Webb et al. 2007; Borregaard and Rahbek 2010). Furthermore, most AOR studies assume relationships remain constant over relatively short time frames (e.g. Maclean et al. 2011; Gutiérrez et al. 2013).

Several hypotheses have been proposed to explain the existence and nature of AORs, which can be divided into three categories (Faulks et al. 2015): (1) niche breadth in relation to abiotic and/or biotic factors (Brown 1984; Holt et al. 1997; Freckleton et al. 2006); (2) population dynamics mediated by dispersal and colonisation (Freckleton et al. 2005; Werner et al. 2014); and (3) sampling artefacts resulting from range position and the resolution of sampling (Gaston et al. 2000; He and Gaston 2000; Wilson 2011). Importantly, these mechanisms are not mutually exclusive (Faulks et al. 2015) and a common thread connecting these hypotheses, explicitly or implicitly, is the degree of spatial aggregation at multiple spatial scales (Storch et al. 2008).

Similar to AOR studies, the association between occupancy (or probability of occurrence) predictions from SDMs and abundance is also usually assumed to be positive and in most cases constant. This has important implications for interpreting SDMs, particularly for species with variable geographic range sizes. Understanding if, and how, this relationship

varies for highly mobile, migratory and nomadic species may increase our understanding of the ecological processes that give rise to them, and improve conservation planning.

The life cycles of many migratory and nomadic species overlap with multiple jurisdictional boundaries (eg. national, state and local governments) and/or land tenures (eg. public, private and reserved land). From a legislative perspective this can result in a complex and often opaque legislative environment to initiate and undertake necessary conservation actions. In particular, the roles or responsibilities of various stakeholders (eg. government agencies, NGOs and industry) and the interpretation of how different (and often conflicting) legislative instruments interact can create significant confusion. If required conservation actions (eg. habitat protection) are also in direct conflict with economic interests (e.g. industrial scale logging), implementing conservation management plans can hit seemingly impassable 'road blocks' leading to paralysis in decision-making for conservation planning and actions. To move from conservation paralysis to action requires an understanding of the reasons why inaction prevails (Meek et al. 2015).

Thesis structure and rationale

The aim of this thesis was to increase our understanding of the spatial ecology of a critically endangered nomadic migrant by developing a population level monitoring program to inform a landscape-scale conservation management strategy, and provide a case study that could inform management and conservation of species with similarly variable distributions.

Each chapter in this Thesis is written in the form of a self-contained scientific paper each with its own comprehensive Introduction, Methods, Results and Discussion. Chapters 2, 3, and 4 are published in the journals Emu, Biological Conservation and Conservation Biology respectively. Chapter 5 has been submitted to the journal American Naturalist.

Study Species

The critically endangered Swift Parrot (*Lathamus discolor*) breeds only in Tasmania during the Austral summer, and relies on tree-hollows of eucalypts for nesting and the flowering of the Tasmanian blue gum (*Eucalyptus globulus*) and black gum (*Eucalyptus ovata*). The nectar from these flowers provides the primary food resource during this time (Brown 1989; Brereton et al. 2004). In eastern Tasmania the species' breeding range largely mirrors the natural range of Tasmanian blue gum, with the exception of the Eastern Tiers (identified during this study) where black gum provides the primary food source. Isolated breeding records have also been recorded in north-western Tasmania, where they rely on black gum and planted Tasmanian Blue Gum (Brown 1989; Mallick et al. 2004). After breeding, Swift Parrots migrate to mainland Australia where they overwinter until returning to Tasmania in early spring (Saunders and Heinsohn 2008).

Prior to this research, knowledge on the spatial ecology of swift parrots within their breeding range was rudimentary. Brown (1989) provided a sound basis to build on our knowledge of the species breeding ecology. However, subsequent conservation management documents (e.g. Brereton 1997, Bryant and Jackson 1999) failed to account for several key aspects of the species ecology, including: (i) key breeding regions and

habitats (eg. wet forest), (ii) the spatially structured nature of breeding events due to patterns in tree flowering, and (iii) dramatic variation in the availability and spatial location of habitat from year to year.

Historical land clearance and timber harvesting dramatically reduced the extent and quality of breeding habitat (Swift Parrot Recovery Team 2001). Failure to account for key aspects of the species spatial ecology when breeding also coincided with the advent of industrial scale logging in Tasmania in more recent decades. This resulted in continued and massive loss of breeding habitat without an appreciation of the importance of particular locations and the broader implications of this habitat loss for the species. During the course of this study another key threat was also discovered, nest predation by the introduced sugar glider (Stojanovic et al. 2014) which synergistically interacts with habitat loss and led to the species being up-listed from Endangered to Critically Endangered (Heinsohn et al. 2015).

In the context of continuing habitat loss as described above, key questions for land managers include:

1. How much habitat needs to be protected to conserve the swift parrot?
2. What is the relative availability and spatial configuration of different functional habitats (foraging and nesting) across the species breeding range?
3. How does the variable distribution of the species affect exposure to nest predation?

The impetus for this study was to provide a detailed assessment of the spatial ecology and breeding requirements of the swift parrot to assist in answering these questions. Specifically, the aims of this research were (i) to quantify tree-level attributes of nesting habitat (Chapter 2), (ii) develop robust sampling and analytical approaches to monitor the species' variable distribution (Chapter 3), (iii) quantify spatiotemporal variation and spatial structuring in both the swift parrot distribution and tree flowering (Chapter 3), (iii) quantify annual variation in the relative availability of functional habitats (i.e. foraging and nesting habitat) (Chapter 4), (iv) examine key elements of the spatial and temporal abundance-occupancy relationships and incorporate them into distribution models (Chapter 5), and (v) provide baseline information to document and quantify trends in abundance and exposure to non-habitat related threats such as nest predation (Chapters 3, 4 & 5).

A better understanding of these topics are crucial to developing spatially explicit, effective conservation planning for the swift parrot primarily through identifying key sites and habitats, and how they change over time. Prior to this study conservation management and knowledge on the spatial ecology for the swift parrot was very rudimentary. Hence conservation management approaches were more suitable for sedentary species whose geographic ranges are more predictable.

CONTEXT STATEMENT

This thesis quantifies spatiotemporal patterns in swift parrot distribution and abundance over ecologically relevant spatial and temporal scales. As stated above it is written in the context of each chapter being a self-contained scientific paper and is in accordance with

the Fenner School of Environment and Society guidelines for a Thesis by Compilation. Each chapter has been published in the chronological order as presented in the thesis (noting Chapter 5 is currently under the submission process). An outline of the rationale for each Chapter and the relationship between Chapters is provided below.

Chapter 1: In the Introduction of this thesis I discuss the global challenges facing conservation planning for highly mobile migratory species. I describe the species which is the focus of this research and outline its basic ecological requirements, knowledge gaps and conservation challenges. Specific challenges relating to understanding the species' spatial ecology, its primary threats, and the study system are discussed in the context of the research contained in the thesis.

Chapter 2: In this chapter I describe and quantify the physical attributes of swift parrot nesting trees. Prior to this research there was little information on the nesting behaviour of swift parrots and in consequence, conservation management was very rudimentary. From a land management perspective, nesting trees had not been previously described and the only protection afforded to swift parrot nesting habitat was known nest sites (i.e. point records. However, no formal surveys or monitoring program were being conducted for nesting swift parrots. Findings from this chapter provided quantitative descriptions of the characteristics of swift parrot nesting trees and identified clear aggregating behaviour (i.e. spatial structuring in nesting) which appeared to be related to local tree flowering conditions. The apparent spatial structure of nests found in this study identified a clear

need to both quantify, and identify the causal factors of spatial structuring of the population across its breeding range.

Chapter 3: Despite previous efforts, there was no effective survey method or monitoring program for the swift parrot prior to this study. Indeed, few population-level monitoring programs exist for similarly highly mobile and nomadic species. In this Chapter I addressed these deficiencies by reporting on increased and focused monitoring efforts in one functional habitat (i.e. foraging habitat) where the species was more detectable. By developing a sampling protocol that maximised detectability while minimising the time taken to visit a site, I devised a monitoring program to survey the entire breeding range (~1000 sites) and analyse the data within an occupancy modelling framework that accounted for imperfect detection.

The results highlighted dramatic changes in the spatial location and extent of the species' distribution that were driven largely by the flowering patterns of *E. globulus and E. ovata*. The novel analytical approach incorporated Generalised Additive Models into a spatially explicit zero-inflated Binomial occupancy modelling framework and revealed significant spatial autocorrelation in both occupancy and detection, which also varied between years. Importantly, the results demonstrated only a fraction of the breeding range was available in most years. The link between occupancy and detectability suggested both parameters were influenced by abundance (also see Chapter 5). The obvious next step of my research (Chapter 4) was to examine how the species variable distribution affects the availability of both functional habitats (i.e. foraging and nesting habitat).

Chapter 4: The complex interactions between the variable distribution of a species and the relative availability of functional habitats can confound effective conservation planning. Therefore, understanding the relationship between available functional habitats and the observed (or predicted) distribution of a species and how this changes over time, is crucial to effective conservation planning. In this Chapter I used the spatially explicit occupancy models from Chapter 3 (with an additional 2 years data) to identify 'key' locations in each year. Using a binary map of 'presence-absence' generated from the occupancy and abundance probability surfaces), and two spatial layers representing the species two functional habitats, I estimated the extent of occupied habitat over six consecutive years.

In this chapter I also tested if the occupancy models (derived from sampling foraging habitat) provided an accurate representation of occupied nesting habitat. The presence-absence of swift parrots was recorded in potential nesting habitat (using tree descriptions described in Chapter 2) using the occupancy models as a spatial guide for surveys sites each year. I built simple constant occupancy models which demonstrated consistently high occupancy rates in nesting habitat in all years (except 2014). Given the dynamic variation observed in the availability of functional habitats each year, I hypothesised the abundance-occupancy relationship would also vary between years (see Chapter 5).

Usually only presence data is available for modelling species with dynamic distributions, and many studies have relied heavily on climatic spatial data layers. In Chapter 4 I also examined the differences in model outputs from presence-only modelling (primarily relying on climatic data) and the occupancy models developed in Chapter 3 (which use

presence-absence data and a direct measure of food availability). Despite using the same dataset (i.e. the presence records) the occupancy models produced significantly smaller (up to an order of magnitude) and more spatially discrete estimates of occupied habitat than models that were only based on climatic factors. This highlights the importance of critically evaluating the data available for modelling species distributions and the modelling techniques employed.

Chapter 5: Conservation planning is heavily reliant on species distribution models and usually assumes a positive and relatively constant relationship between occupancy (or other habitat suitability indices) and abundance. Because of the extreme spatiotemporal variation in the species distribution a logical next step for my research was to examine the abundance-occupancy relationship. Using data from Chapters 3 and 4 (plus an additional year's data) I tested the hypothesis that the temporal abundance-occupancy relationship was negative. Under this hypothesis, as the proportion of occupied sites decreases the average density of individuals over occupied sites should increase. I also tested the hypothesis that the relationship between abundance and predicted occupancy should be positive, but variable between years depending on the availability of food resources. In both cases these hypothesis were supported by empirical data that I had collected. In this context, this Chapter provides an extremely rare example of the abundance-occupancy relationship for a nomadic resource specialist, which has broad implications for conservation planning for this group of species more generally.

Chapter 6: To conclude, I discuss the findings of this research in the context of understanding and monitoring spatiotemporal patterns in species with highly variable distributions. I discuss the relevance of my results to conservation planning for mobile species and how similar research may be achieved for other difficult to study species.

In the context of swift parrot conservation, I synthesise the importance of my research to conservation planning relating to ongoing loss of breeding habitat, natural variability in the availability of habitat, and exposure to predation by the introduced sugar glider.

REFERENCES

Araújo MB, and Luoto M. (2007). The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography*, **16:**743-753.

Bailey, L. L., Simons, T. R., Pollock, K. H. (2004). Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications*, 14, 692-702.

Barçante, L., M. M. Vale, and M. A. S. Alves. (2017). Altitudinal migration by birds: a review of the literature and a comprehensive list of species. *Journal of Field Ornithology*, 88, 321-335

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., and Ferrer, E.A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51-57.

Bastille-Rousseau, G., J. A. Gibbs, J. P., C B. Yackulic, J. L. Friar, F. Cabrera, L. P. Rousseau, , M. Wikelski, et al. (2017). Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system. *Oikos*, 126, 1004-1019

Bini, L. M., Diniz, J. A. F., Rangel, T., Akre, T. S. B., Albaladejo, R. G., Albuquerque, F. S., Aparicio, A., Araujo, M. B., Baselga, A., Beck, J., Bellocq, M. I., Bohning-Gaese, K., P. A. V. Borges, P. A. V., Castro-Parga, I., Chey, V. K., Chown, S. L., de Marco, P., Dobkin, D. S., Ferrer-Castan, D., Field, R., Filloy, J., Fleishman, E.,

Gomez, J. F., Hortal, J., Iverson, J. B., Kerr, J. T., Kissling, W. D., Kitching, I. J., Leon-Cortes, J. L., Lobo, J. M., Montoya, D., Morales-Castilla, I., Moreno, J. C., Oberdorff, T., Olalla-Tarraga, M. A., Pausas, J. G., Qian, H., Rahbek, C., Rodriguez, M. A., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N. J., Terribile, L. C., Vetaas, O. R., Hawkins, B. A.. 2009. Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. Ecography 32, 193-204.

Borregaard, M. K., and C. Rahbek. 2010. Causality of the relationship between geographic distribution and species abundance. Quarterly Review of Biology 85:3-25.

Boyle, W. A. 2008. Partial migration in birds: tests of three hypotheses in a lekking frugivore. Journal of Animal Ecology 77:1122-1128

Boyle, W. A. 2011. Short-distance partial migration of Neotropical birds: a community- level test of the foraging limitation hypothesis. Oikos 120:1803-1816

Brambilla M, Saporetti F. 2014. Modelling distribution of habitats required for different uses by the same species: Implications for conservation at the regional scale. Biological Conservation **174:**39-46.

Brereton, R. (1997). Management Prescriptions for the Swift Parrot in Production Forests. Report to the Tasmanian RFA Environment and Heritage Technical Committee.

Brereton, R., Mallick, S.A., and Kennedy, S.J. (2004). Foraging preferences of Swift Parrot on Tasmanian Blue-gum: tree size, flowering frequency and flowering intensity. *Emu*, **104**, 377-383.

Brown, J. H. 1984. On the Relationship between Abundance and Distribution of Species. The American Naturalist 124:255-279.

Brown, P.B. (1989). The Swift Parrot *Lathamus discolor*: A report on its ecology, distribution and status, including management considerations. Report to the Department of Lands Parks and Wildlife.

Bryant, S. L. and Jackson, J. (1999). Tasmania's Threatened Fauna Handbook: what, where and how to protect Tasmania's threatened animals. Threatened Species Unit, Parks and Wildlife Service, Hobart.

Buckley, H. L., and R. P. Freckleton. (2010). Understanding the role of species dynamics in abundance–occupancy relationships. *Journal of Ecology*, 98, 645-658

Buckley, S. M., R. H. Thurstan, A. Tobin, and J. M. Pandolfi. (2017). Historical spatial reconstruction of a spawning-aggregation fishery. *Conservation Biology*, 31:1322-1332

Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J. J., Southwell, D. M., Armstrong, D. P., Chadès, I., Lacy, R. C., and Converse, S. J. (2015). When do we need more data? A primer on calculating the value of information for applied ecologists. *Methods in Ecology and Evolution*, DOI: 10.1111/2041-210X.12423

Cottee-Jones, H.E.W., Matthews, T.J. & Whittaker, R.J. (2016). The movement shortfall in bird conservation: accounting for nomadic, dispersive and irruptive species. *Animal Conservation*, 19, 227-234.

Dingle, H. 2008. Bird migration in the southern hemisphere: a review comparing continents. Emu 108:341-359.

Dormann, C. F. (2007). Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, 16, 129-138. ecology. *Journal of Animal Ecology*, 79, 933–936.

Faulks, L., R. Svanbäck, H. Ragnarsson-Stabo, P. Eklöv, and Ö. Östman. (2015). Intraspecific Niche Variation Drives Abundance-Occupancy Relationships in Freshwater Fish Communities. *The American Naturalist*, 186, 272-283.

Freckleton, R. P., D. Noble, and T. J. Webb. (2006). Distributions of habitat suitability and the abundance-occupancy relationship. *American Naturalist*, 167, 260-275.

Freckleton, R. P., J. A. Gill, D. Noble, and A. R. Watkinson. (2005). Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. *Journal of Animal Ecology*, 74, 353-364.

Gaston KJ, and Fuller, RA. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*, 46, 1-9.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology*, 37, 39-59.

Gibson, L. A. (2011). The importance of incorporating imperfect detection in biodiversity assessments: a case study of small mammals in an Australian region. *Diversity and Distributions*, 17, 613-623.

Gu, W., Swihart, R. K.. (2004). Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biological Conservation*, 116, 195-203.

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kajula, H, Lentini PE, McCarthy MA, Tingley R, Wintle BA. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*, 24, 276-292.

Guisan A, Zimmerman N. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling*, 135, 147-186.

Gutiérrez, D., J. Harcourt, S. B. Díez, J. Gutiérrez Illán, and R. J. Wilson. (2013). Models of presence - absence estimate abundance as well as (or even better than) models of abundance: the case of the butterfly Parnassius apollo. *Landscape Ecology*, 28, 401-413.

Hastie T, Fithian W. (2013). Inference from presence-only data; the ongoing controversy. *Ecography*, 36, 864-867.

Hawkins, B. A. (2012). Eight (and a half) deadly sins of spatial analysis. *Journal of Biogeography*, 39, 1-9.

Heinsohn R, Webb M, Lacy R, Terauds A, Alderman R, Stojanovic D. 2015. A severe predator-induced population decline predicted for endangered, migratory swift parrots (*Lathamus discolor*). *Biological Conservation,* **186:**75-82.

Holt, R. D., J. H. Lanwton, K. J. Gaston, and T. M. Blackburn. (1997). On the relationship between range size and local abundance: Back to basics. *Oikos*, 78, 183-190.

Hui, C., McGeoch, M. A., and Warren M. (2006). A spatially explicit approach to estimating species occupancy and spatial correlation. *Journal of Animal Ecology*, 75, 140-147.

Jetz W, Sekercioglu CH, and Watson JEM. (2008). Ecological correlates and conservation implications or overestimating species geographic range sizes. *Conservation Biology*, 22:110-119.

Kalle, R., T. Ramesh, and C.T. Downs (2018). When and where to move: Dynamic occupancy models explain the range dynamics of a food nomadic bird under climate and land cover change. *Global Change Biology*, DOI: 10.1111/gcb.13861

Kéry, M., Guillera-Arroita, G., and Lahoz-Monfort, J. J. (2013). Analysing and mapping species range dynamics using occupancy models. *Journal of Biogeography*, 40, 1463-1474.

Lahoz-Monfort, J.J., Guillera-Arroita, G., and Wintle, B.A. (2014) Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography*, 23, 504-515

Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659-1673.

Lichstein, J. W., Simons, T. R., Shriner, S. A., and Franzreb, K. E. (2002). Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, 72, 445-463.

MacKenzie D, Nichols JD, Lachman GB, Droege S, Royle JA, and Langtimm CA. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248-2255.

Maclean, I. M. D., R. J. Wilson, and M. Hassall. 2011. Predicting changes in the abundance of African wetland birds by incorporating abundance–occupancy

relationships into habitat association models. *Diversity and Distributions*, 17, 480-490.

Mallick, S., James, D., Brereton, R., and Plowright, S. (2004). Blue-gums *Eucalyptus globulus* in north-west Tasmania: an important food resource for the endangered Swift Parrot *Lathamus discolor. Victorian Naturalist,* **101**, 36-46.

Martin, T., Wintle, B., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., A. Tyre, A. J., H. and Possingham, H. P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters*, 8, 1235-1246.

Meek, M. H., Wells, C., Tomalty, K. M., Ashander, J., Cole, E. M., Gille, D. A., Putman, B. J., Rose, J. P., Savoca, M. S., Yamane, L., Hull, J. M., Rogers, D. L., Rosenblum, E. B., Shogren, J. F., Swaisgood, R. R., and May, B. (2015). Fear of failure in conservation: The problem and potential solutions to aid conservation of extremely small populations. *Biological Conservation,* **184**, 209-217.

Newton, I., 2006. Advances in the study of irruptive migration. *Ardea*, 94, 433-460

Phillips S, Anderson R, and Schapire R. (2006). Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, 190, 231–259.

Royle, J. A., and Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, 84, 777-790.

Runge, C. A., T. G. Martin, H. P. Possingham, S. G. Willis, and R. A. Fuller. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, 12:395-402.

Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015). Protected areas and global conservation of migratory birds. *Science*, 350, 1255.

Saunders, D. L., and Heinsohn, R. (2008). Winter habitat use by the endangered, migratory Swift Parrot (*Lathamus discolor*) in New South Wales. *Emu*, **108**, 81-89.

Sekercioglu, C.H. (2010). Partial migration in tropical birds: the frontier of movement

Stojanovic, D., Webb, M., Alderman, R., Porfirio, L. & Heinsohn, R. (2014). Discovery of a novel predator reveals extreme but highly variable mortality for an endangered bird. *Diversity and Distributions*, 20, 1200-1207

Storch, D., A. L. Šizling, J. Reif, J. Polechová, E. Šizlingová, and K. J. Gaston. (2008). The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecology Letters*, 11:771-784.

Swift Parrot Recovery Team (2001). Swift Parrot Recovery Plan. Department of Primary Industries Water and Environment, Hobart.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false negative error rates. *Ecological Applications*, 13, 1790-1801

Vanreusel W, Maes D, van Dyck H. (2007). Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology*, 21, 201-212.

Webb, T. J., D. Noble, and R. P. Freckleton. (2007). Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *Journal of Animal Ecology*, 76, 123-134.

Werner, E. E., C. J. Davis, D. K. Skelly, R. A. Relyea, M. F. Benard, and S. J. McCauley. 2014. Cross-scale interactions and the distribution-abundance relationship. *PLoS One*, 9:e97387

Wintle, B. A., McCarthy, M. A., Parris, K. M., and Burgman, M. A. 2004. Precision and bias of methods for estimating point survey detection probabilities. *Ecological Applications*, 14, 703-712.

CHAPTER 2: Nesting requirements of the endangered Swift Parrot

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ABSTRACT

Declines in avian biodiversity are being reported worldwide. A better understanding of the ecology of many species is fundamental to identifying and addressing threatening processes and developing effective mitigation measures. The Swift Parrot is an endangered obligate migratory species that only breeds in Tasmania. The species nests in tree hollows and forages primarily on flowers of the Tasmanian blue gum (*Eucalyptus globulus*) and black gum (*Eucalyptus ovata*) during the breeding season. Surveys for Swift Parrot nests conducted over three consecutive breeding seasons identified 130 Swift Parrot nests in 117 nest trees. Swift Parrot nest trees were characterised as being large eucalypts (mean DBH=100 cm) with five or more potential hollows (mean=8.6) and showing clear signs of senescence. Nests were found singly and in clusters of up to 49 nests. Nest reuse was uncommon and most likely related to poor blue gum flowering surrounding nest sites in subsequent years. Given the temporal nature of Swift Parrot breeding habitat the provision of potential nesting sites for aggregations of breeding pairs at a single site is recommended. This requires the management or reservation of suitable forest stands with old-growth characteristics across the landscape rather than focussing on individual trees or historical nest sites.

INTRODUCTION

The Swift Parrot (*Lathamus discolor* White) only breeds in Tasmania between September and January in tree hollows of eucalypt species (Brown 1989). After breeding the birds migrate to mainland Australia where they over-winter until returning to Tasmania in early spring (Brown 1989). The Swift Parrot breeding season coincides with the flowering period of the Tasmanian blue gum (*Eucalyptus globulus*) and black gum (*Eucalyptus ovata*). The nectar from these flowers is the primary foraging resource during this time (Brown 1989; Brereton 1997).

The known breeding distribution of the Swift Parrot in eastern Tasmania falls within the natural range of *E. globulus* (Williams and Potts 1996; Brereton 1997). The Swift Parrot also breeds in northwest Tasmania outside the natural range of *E. globulus* where they rely largely on *E. ovata* and planted *E. globulus.* (Brown 1989; Mallick *et al.* 2004). Although *E. globulus* is recognised as key foraging habitat for the Swift Parrot, spatio-temporal patterns in flowering are not well understood and it may be years between flowering events (Tilyard and Potts 2003; Brereton *et al.* 2004; Mallick *et al.* 2004). There is little information on how these flowering patterns affect the distribution of Swift Parrot nesting from year to year.

Brereton (1997) provided the most detailed description of Swift Parrot nest site characteristics, based on 46 nest sites recorded between 1981 and 1995, although detailed

information was available for only 24 of these. Information from a further 17 nests was obtained from the Swift Parrot egg collection of R.H. Green (Brown 1989). Nests were predominantly in *Eucalyptus obliqua*, *Eucalyptus pulchella* and *E. globulus* with a diameter at breast height (DBH) greater than 70 cm (mean 120 cm, range 50-305 cm). Brereton (1997) noted examples of up to 5 pairs nesting in close proximity to each other and suggested that nest site selection in any particular year was related to the proximity of foraging sites.

Swift Parrot breeding habitat has been reduced in area and quality through clearance for agriculture, timber harvesting and urban development (Garnett and Crowley 2000; Swift Parrot Recovery Team 2001). The most recent population estimate of Swift Parrots is <1000 breeding pairs (Swift Parrot Recovery Team 2001). The species is listed as Nationally Endangered under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999.*

Over the decade prior to 2010, protection of foraging habitat was the major focus of Swift Parrot conservation efforts in Tasmania (eg. Brereton *et al.* 2004; Mallick *et al.* 2004; Munks *et al.* 2004). Activities regulated through the Forest Practices System in Tasmania were required to protect known Swift Parrot nest sites through the application of a 1 ha reserve around a known nest (Brereton 1997; Jackson and Munks 1998). In recent years, the protection of known nest sites has been considered on a case-by-case basis. The

public and private reserve system in Tasmania has also provided protection to some known nest sites.

Given the paucity of data on the breeding habitat requirements of the Swift Parrot, the aim of this study is to provide a detailed assessment of nest site characteristics, focussing on tree-level descriptions that can be used to assist field workers in the identification of potential nesting habitat. We also examined the spatial distribution of nests and reuse of nesting sites.

MATERIALS AND METHODS

Nest survey sites

Targeted surveys were conducted in southeast Tasmania within the natural range of *E. globulus*. Historical Swift Parrot nest sites were visited early in the breeding season (September-October) and survey sites were selected based on the presence of Swift Parrots. Nest surveys were conducted during November and December each year. In 2004, two sites where Swift Parrots were present were intensively surveyed for nests (Fern Tree and Maria Island) (Figure 1). Approximately 50 ha of forest were searched over three weeks at Fern Tree, 12 ha of forest were searched over two days on Maria Island. In 2005, two additional sites were surveyed for nests (Bruny Island and Meehan Range) and nest trees were checked for reuse at Fern Tree and Maria Island. Approximately 90 ha of forest were searched over 3 weeks on Bruny Island, and 130 ha over 4 weeks in the Meehan Range. Time constraints limited the area searched on Maria Island. Permission to access private property and the distribution of trees with potential

hollows influenced the extent of the area searched at all other sites. In 2006 nest trees were checked for reuse at all sites. Where practicable, all trees containing potential hollows within each site were searched for the presence of nests following the sampling protocol outlined below.

Forest at all sites comprised a range of tree age classes from young regrowth to senescent or dead trees. Forest types were as follows (Harris and Kitchener 2005): Fern Tree - dry *E. obliqua* interspersed with dry *E. pulchella* forest, Maria Island - wet and dry *E. obliqua* forest with *E. globulus* and *E. viminalis* trees occurring as sub-dominant or locally dominant in some patches, Bruny Island - dry *E. pulchella* forest/woodland with *E. globulus* trees occurring as subdominant or locally dominant in some patches, Meehan Range - dry *E. pulchella* and dry *E. globulus* forest and woodland with Dry *Eucalyptus tenuiramis* and dry *E. amygdalina* forest/woodland common in the surrounding area.

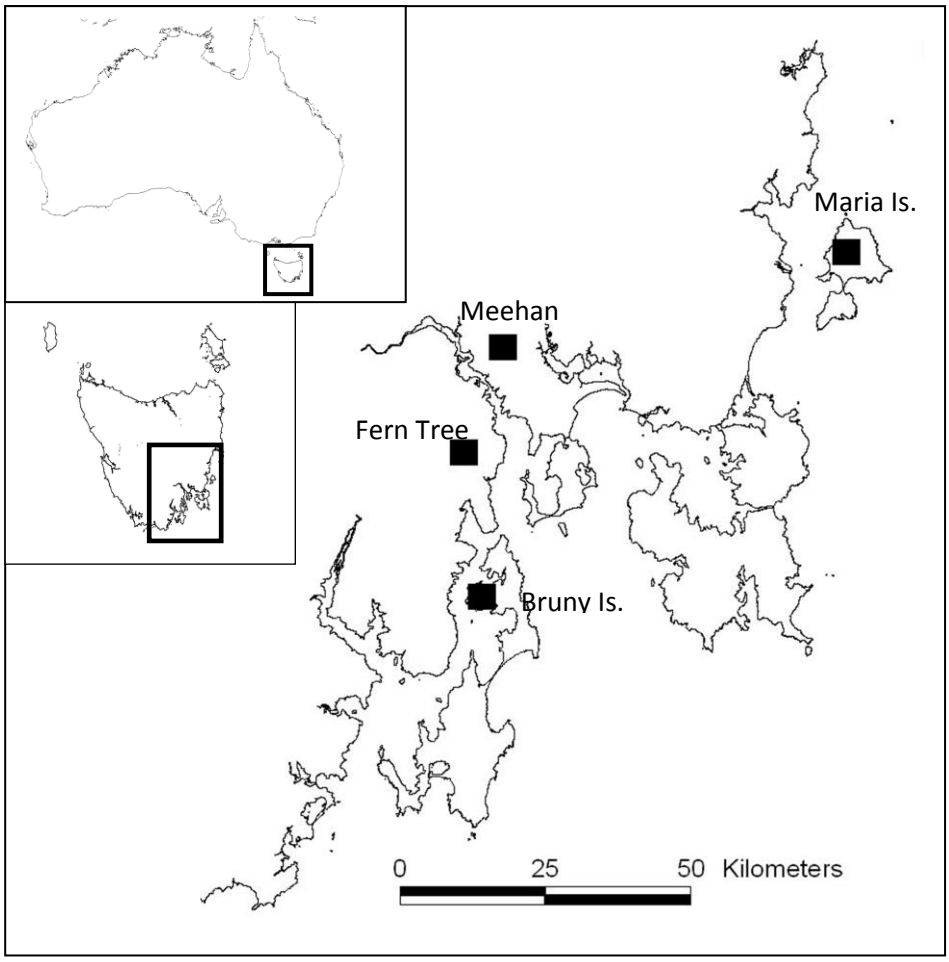

Figure 1. Location of 4 study sites where Swift Parrot nest surveys were conducted in southeast Tasmania, Australia.

Sampling protocol

Nest searching began at a random starting point at each site. Nest searching radiated out in all directions from this initial starting point. All trees within an approximate 100m

radius of a sampling point (depending on visibility and terrain), were searched for 3.5 hours. Trees containing potential hollows within each site were searched for the presence of nests. At sites 1, 3, and 4 further nest searching was conducted along a roaming point transect line extending away from each intensively searched area. Sampling points along the transect were selected by the presence of trees with potential hollows. The direction and length (0.5-3.5 km) of each transect was largely determined by land tenure preventing access and the distribution of trees with potential hollows. In 2004 and 2005 nest searching was abandoned once large numbers of Swift Parrot fledglings appeared in late December.

A tree was considered a nest tree when one or more of the following behaviours were observed:

- An adult female was fed by a male and returned directly to a hollow where she remained;
- A single adult bird was seen entering a hollow (showing no interest in any other hollow) on more than two occasions;
- Chicks were observed being fed by an adult at a hollow entrance.

Nests were checked for reuse in the following year(s). While checking for nest reuse, the presence of Swift Parrots at the general site was also recorded.

Random tree selection

For each nest tree a random 'non-nest' tree was selected as a case control to compare selected variables. The selection protocol for random trees followed the methods outlined in Manning *et al.* (2004). Briefly, random trees were selected as the nearest tree to a nest tree with a diameter at breast height (DBH) >50 cm on a compass bearing of 30^{o} more than the previous random tree. If a tree was not located on the compass bearing the next tree in a clockwise direction was selected.

Tree variables

The findings of previous studies on hollow occurrence and use by vertebrate fauna (e.g. Saunders *et al.* 1982; Lindenmayer *et al*. 2000; Gibbons and Lindenmayer 2002; Manning *et al.* 2004) were used as a basis for the selection of tree variables and methods used in this study. Variables measured for all trees are listed below.

- Species of tree
- diameter of stem at breast height *c.*1.3m above ground level (DBH)
- tree height (measured using an inclinometer and range finder)
- number of potential hollows observed from all angles from the ground using binoculars (with an estimated entrance size of 4 cm or greater)
- fire scars (0 = none, 1 = burnt bark, 2 = damage to vascular cambium, 3 = large hollow in base of tree)
- presence/absence of dead branch/limb >15cm in diameter

- percentage of dead branches (all sizes) in crown (1 = 0-5%, 2 = 5-20%, 3 = 20-50%, 4 = >50%)
- tree form (1 = apically dominant or rounded crown, 2 = distinct gaps in crown, 3 = dead limbs penetrating a disjunct crown, 5 = dead limbs penetrating almost dead crown, 6 = dead stag)
- aspect (N, NE, E, SE, S, SW, W, NW)
- topographic position (gully, lower slope, mid slope, upper slope, ridge)
- ground slope (1 = 0-5^{o}, 2 = 6-10^{o}, 3 =11-15^{o}, 4 = >15^{o})

Potential hollows were any knotholes, branch stubs and fissures, and any spouts or limbs (>15 cm diameter) with the end broken off. Several studies have reported inaccuracies associated with estimating number of hollows from the ground (see Gibbons and Lindenmayer 2002) and this variable can often result in an over-estimate of hollow abundance. The count of potential hollows was therefore treated as an index of hollow abundance and no attempt was made to distinguish between "real" and "blind" entrances.

Statistical analysis

Because the design employed has the form of a case-control study the analysis is based on differences in characteristics of the paired trees (i.e. each tree that contains a nest is compared with the neighbouring matched tree that does not have a nest). Each matched pair becomes a unit in a stratum and with two distinct levels of comparison, within-pair and between-pair comparisons. It is the within-pair differences that are of interest in this

study. The response is binary (i.e. nest presence or absence) and the aim was to determine the extent to which the odds of a tree having a nest is related to the recorded tree characteristics. Thus, logistic regression analysis is an appropriate method to employ. However, standard (unconditional) logistic regression analysis is not appropriate because it requires independent selection of trees (i.e. a one-stratum design). The method appropriate for a case-control design is known as conditional logistic regression analysis (Breslow and Day 1980), which makes separate comparisons of nest and non-nest trees within each pair.

The analysis used the NOMREG procedure in SPSS to fit conditional logistic regression analysis. Likelihood ratio tests were employed to test for evidence of a relationship between the odds of a tree having a nest and an explanatory variable. Because the analysis is based on differences, the use of qualitative explanatory variables with more than two levels is precluded. Such variables were transformed into two or more contrasts for inclusion. Thus, the qualitative explanatory variables reported in Table 2 were necessarily grouped into binary variables. Stepwise regression analysis is based on a likelihood ratio statistic for inclusion and exclusion.

RESULTS

Nest tree characteristics

One-hundred and thirty Swift Parrot nests in 117 nest trees were identified over three consecutive breeding seasons. Reused nest trees or trees with more than one nest or nest

hollow were included only once in the analysis. The mean number of potential hollows per tree was 8.6 (range = 2-22) for nest trees and 2.1 (range = 0-11) for random 'non-nest' trees (Figure 2). The mean DBH of trees was 105 cm (range = 33-202) for nest trees and 76 cm (range = 50-174) for random 'non-nest' trees (Figure 3). Mean nest tree height was 23 m (range = 10-45) and mean random tree height was 20 m (range 12-35). Although tree height was a significant variable, there was considerable overlap in their distributions (Figure 4). Only *E. obliqua*, *E. pulchella* and *E. globulus* had sufficient sample sizes to be included in the analysis of tree species. Aspect was omitted from the analysis because the aspect of non-nest trees was correlated with the aspect of the paired nest tree. Nest trees were found on all aspects with 43% being on south or south west facing slopes. The higher incidence of these aspects was related to a sampling bias towards these aspects. Frequencies of other qualitative variables are shown in Table 2.

Table 1. Results of conditional logistic regression analysis testing for differences between nest trees and random trees. Only explanatory variables having a p-value less than 0.01 are included.

Variable	Significance. from LR test	Estimated odds ratio	95% Confidence Interval for odds ratio	
			Lower Bound	Upper Bound
Number of hollows	<0.0001	3.2	1.8	5.7
DBH	<0.0001	1.05	1.03	1.1
Generally healthy: no vs yes	<0.0001	10.5	4.5	24.3
Tree form: 1, 2, 3 vs 4 & 5	<0.0001	16.7	6.1	45.9
% dead branches: <20% vs 20% or more	<0.0001	6.1	3.1	11.9
Hollow from fire scar: yes vs no	<0.0001	5.9	2.9	11.9
Dead limb or tree: present vs absent	<0.0001	14.0	4.3	45.2
Healthy: no vs yes	<0.0001	44.0	6.1	319.4
Fire scar: none vs some	<0.0001	7.0	2.5	20.0
Tree height	<0.0001	1.12	1.05	1.2

The relative likelihood of a tree containing a Swift Parrot nest was significantly associated with seven of the 10 variables when modelled individually (Table 1). A tree was 3.2% more likely to be a nest tree with each additional potential hollow. A tree was 1% more likely to contain a nest for every 1 cm increase in DBH. Trees with dead limbs penetrating a disjunct crown or and almost dead crown were, on average, 16.7 times more likely to contain a nest than other tree forms. Trees with >20% dead branches in the

crown were, on average, 6.1 times more likely to contain a nest. Trees with at least one dead limb (including dead stags) were, on average, 14 times more likely to contain a nest. Trees were, on average, (7 and 5.9 times) more likely to contain a nest if they were fire scarred or had a hollow base from fire scarring, (respectively). With every increase in tree height of 1 m trees were (1.1%) more likely to contain a nest.

The stepwise fitting of explanatory variables found no additional information is added to the model beyond the number of hollows. This implies there is a high level of correlation among variables.

Nest hollows

One hundred and twenty-eight nest hollows were described from 117 nest trees. Nest hollows were more frequently found in branches (70%) compared to the main stem, and in hollows with knothole or branch stub entrances (68%) compared to spouts or fissures. Entrance aspects of nest hollows (n = 127) were relatively evenly distributed. The characteristics of nest hollows are shown (Table 3). Mean height above ground of nest hollow entrances was 14 m (range = 5-40) with 82% between 6-20 m.

Tree martins (*Hirundo nigricans*), Green Rosellas (*Platycercus caledonicus*) and Australian Owlet-nightjars (*Aegotheles cristatus*) were observed using nest hollows after being vacated by Swift Parrots and in following years when not in use by Swift Parrots.

Table 2. Frequency table of qualitative variables for 117 paired random and nest trees.

Variable	Random tree	Nest tree
Species		
E. obliqua	32	25
E. globulus	40	31
E. pulchella	36	41
E. viminalis	0	4
E. tenuiramis	2	2
E. amygdalina	4	0
dead stag	3	14
Dead limbs		
no	43	4
yes	71	99
dead trees	3	14
% dead branches in crown		
0-5%	37	1
5-20%	48	33
20-50%	25	43
>50%	7	40
Tree form		
apically dominant or rounded crown	25	0
distinct gaps in crown	46	8

Table 2 continued.

dead limbs penetrating crown	41	76
dead limbs penetrating almost dead crown	2	19
dead tree	3	14
Fire damage		
no damage	32	8
presence of burnt bark	24	8
cambium showing clear signs of fire	23	19
large hollow burnt through base of tree	38	82
Topographic position		
gully	3	13
lower slope	15	8
mid-slope	15	12
upper slope	52	49
ridge	32	35
Slope		
0-5	25	24
6-10	28	30
11-15	32	36
>15	32	27

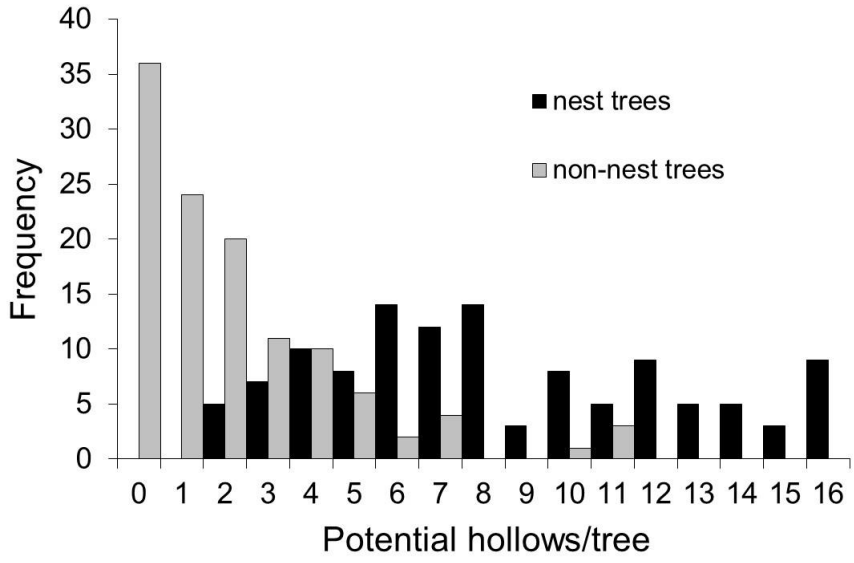

Figure 2. Frequency distribution of potential hollows per tree

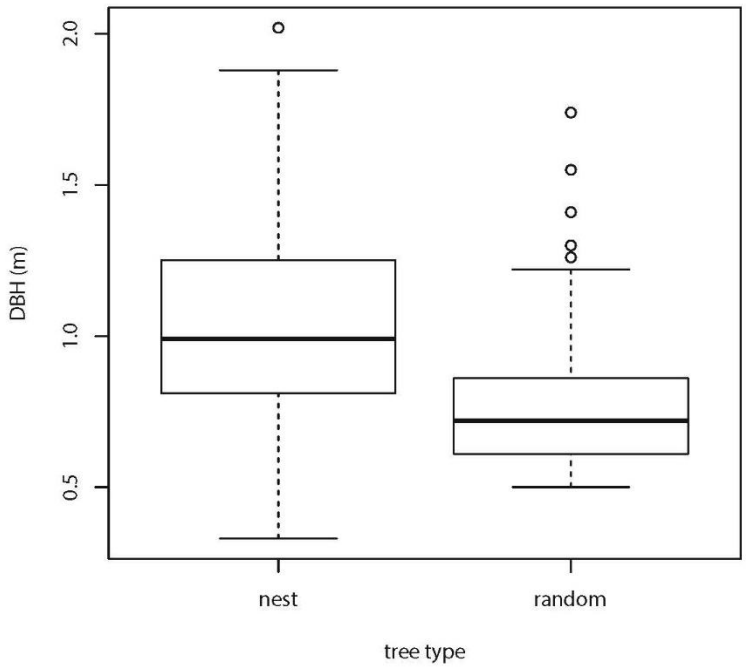

Figure 3. Box plot summarising diameter at breast height (DBH) for Swift Parrot nest trees and random trees

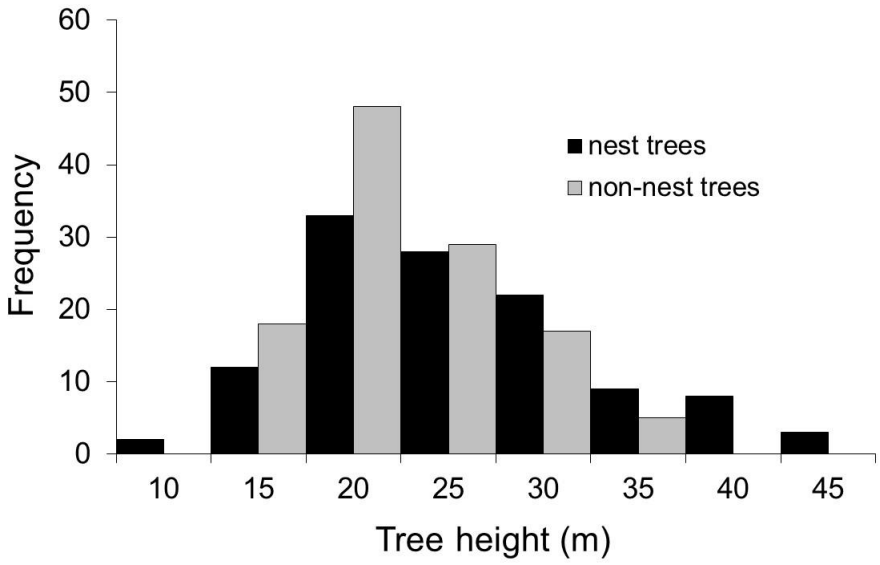

Figure 4. Frequency distribution of tree heights

Table 3. Characteristics of Swift Parrot nest hollows

Variable	Number of nests
Hollow type	
spout	20
knothole/branch stub	87
fissure	21
Position in tree	
branch	90
main stem	38
Aspect	
n	17
ne	15
e	18
se	7
s	22
sw	8
w	9
nw	12
vertical	19

Nest distribution

In 2004, 26 Swift Parrot nests were identified at Fern Tree, and 10 nests at Maria Island. In 2005, 40 nests were identified on North Bruny, 49 nests in the Meehan Range. Three "new nests" were found on Maria Island while checking for reuse of nests from 2004. The spatial arrangement of nest trees at each site is shown in Figure 5. Flowering *E. globulus* trees were common within several kilometres of each site, wherever nests were found, except for one reused nest where no flowering was observed.

Nest reuse

All nests identified in 2004 were checked for reuse in 2005. Only one of 26 nest hollows was reused at Fern Tree. No other Swift Parrots were observed during the entire period of checking for nest reuse and no flowering *E. globulus* trees were observed. On Maria Island only one of 10 nest hollows were reused, although the three "new nests" identified were all within 100 m of the 2004 nest sites. Swift Parrots were regularly observed while checking for nest reuse at this site and flowering *E. globulus* trees were abundant at the site and in the surrounding area.

In 2006, 48% of nests found in 2004 and 2005 were checked for reuse. Fourteen nests were checked at Fern Tree, 10 nests on Maria Island, 20 nests on Bruny Island and 19 nests in the Meehan Range. None of the nests checked were in use by Swift Parrots. No Swift Parrots or flowering *E. globulus* trees were observed at any site.

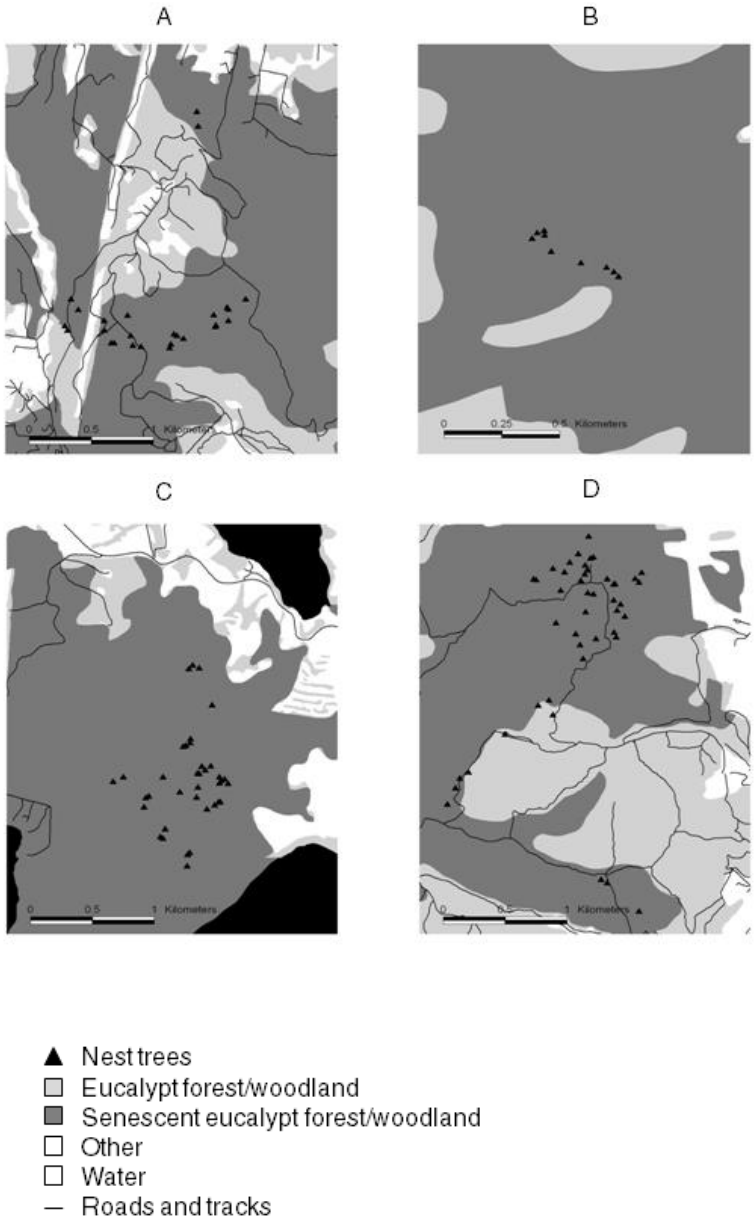

Figure 5. Spatial distribution of nest trees and forest age. A- Fern Tree, B- Maria Is., C- Bruny Is., D- Meehan Range. Eucalypt senescence was obtained from the Tasmanian RFA Forest Senescence Data Layer (Commonwealth of Australia and State of Tasmania 1997).

DISCUSSION

Nest trees

Swift Parrot nest trees were characterised by having five or more potential hollows, a DBH >80 cm, dead limbs penetrating the crown and showing clear signs of senescence. The relative probability of a tree being used as a nest tree by Swift Parrots increased with the number of potential hollows and DBH. The number, size and diversity of hollows in eucalypts are significantly correlated to tree diameter (eg. Bennett *et al.* 1994; Lindenmayer *et al.* 2000; Harper *et al.* 2005). Our results reflect those of other studies that show that as tree size (and number of hollows) increases, so does the probability of a hollow being suitable for a particular species (Gibbons and Lindenmayer 2002; van der Ree *et al.* 2006). Tree health, form and fire damage are recognised as predictors of hollow occurrence in eucalypts and these attributes are often closely correlated with DBH (eg. Saunders *et al.* 1982; Inions *et al.* 1989; Gibbons and Lindenmayer 2002). Manning *et al.* (2004) suggested that DBH alone is a useful field predictor of Superb Parrot (*Polytelis swainsonii*) nest trees. In our study, stepwise regression analysis suggested the explanatory variables for Swift Parrot nest trees are similarly correlated.

The high incidence of nest trees on slopes with southerly and south-westerly aspects is in contrast to Brereton (1997) who reported a high incidence of nest trees on north facing slopes. Considering that nests were found in several *Eucalyptus* species and forest types, nest tree selection is most likely related to the presence of hollows and proximity to a foraging resource.

We provided quantitative evidence that the number of potential hollows per tree, tree diameter, and characteristics relating to tree health and form are an appropriate field method for identifying potential nest trees for Swift Parrots. Counting potential hollows may be suitable for assessing small numbers of trees; however, when assessing potential nesting habitat at the forest stand level we suggest the most efficient method is through a visual audit of tree diameter, tree form and tree health. Given that most nest trees were located in dry forest, verification of these results in wet forest types may be required if the results are to be extended to these forest types.

Nest hollows

Brereton (1997) reported Swift Parrots were more likely to use hollows facing a northerly direction. In contrast, our study suggests the birds will use nest hollows facing any direction. The higher incidence of nest hollows in branches is probably related to a greater abundance of branch hollows. Similarly, the greater incidence of nests in knotholes and branch stubs is most likely related to the availability of these hollow types. The mean nest hollow height (14 m) is similar to that reported by Brown (1989) (13.4 m) and Brereton (1997) (15 m). As suggested by Manning *et al.* (2004) mean nest hollow heights may simply be a function of the size of trees available. For example, tree heights at site 2 were generally larger than at other sites and the mean nest hollow height was 22 m whereas the overall mean was 14 m.

Nest distribution

The area surveyed for nests at each site covered only part of a larger forest patch (> 500 ha) mapped as senescent eucalypt forest by the Tasmanian government (Commonwealth of

Australia and State of Tasmania 1997). This mapping assessed tree crown attributes using features described by Jacobs (1955) such as shrinking crowns, bayonet branches and missing branches (see Commonwealth of Australia and State of Tasmania 1996). These features are indicators of the presence of tree hollows. Therefore, there was potentially several hundred hectares of nesting habitat immediately adjacent to the recorded nest sites that was not surveyed for nests. Assuming that Swift Parrot nests were distributed at similar densities through at least part of this unsurveyed forest, a large proportion of the entire population may have nested at these sites.

Avian nectarivore densities are often closely correlated with patterns of flowering intensity of eucalypts in Australia; however, measuring eucalypt flowering at a scale relevant to many nectarivores can be difficult (Mac Nally and McGoldrick 1997). Although this study did not attempt to quantify eucalypt flowering, general observations of *E. globulus* flowering differed dramatically between years at each site. Hundreds of *E. globulus* trees were in heavy flower at each site when nests were first recorded. When each site was checked for reuse in the following year(s) virtually no flowering was observed except at site 2 where abundant flowering was observed in 2004 and 2005. The lack of nest reuse was most likely (at least in part) due to these dramatic differences in the availability of *E. globulus* flower. The reuse of one nest at site 1 in 2005 was the only record of Swift Parrots present at a site where flowering conditions were apparently poor.

Whilst Swift Parrots are not restricted to breeding in aggregations, we suggest that nesting densities consistent with those observed in our study may not be uncommon events and are

probably driven by the annual flowering patterns of *E. globulus* and the distribution and abundance of hollows at individual sites.

Management Implications

Swift Parrots generally nest in trees with >80 cm DBH, five or more potential hollows and trees that show clear signs of senescence. Nest trees occurred across a range of forest types but their use by Swift Parrots in any given year is correlated with the proximity and/or quality of preferred *Eucalyptus* flowers. Where there is an abundance of food and suitable nest trees in close proximity to each other Swift Parrots nest in aggregations.

Management prescriptions for nesting habitat which largely rely on identifying specific nest trees are unlikely to provide adequate protection for aggregations of breeding Swift Parrots. With considerable survey effort in each breeding season this management approach may be partially effective; however, the resources required to undertake intensive annual surveys effectively are unlikely to be available to nature conservation agencies and land managers.

Published information on hollow formation in eucalypts in Tasmania (e.g. Koch *et al.* 2008) and similar studies from mainland Australia (e.g. Mawson and Long 1994; Stoneman *et al.* 1997) suggest that Swift Parrot nest tree recruitment, and thus the management of nesting and associated foraging habitats, needs to be considered on a time scale of 100's of years.

Our results highlight the importance of microhabitat characteristics for swift parrot nest selection. Understanding how these factors influence the species at the landscape scale should be considered an urgent research priority for this species. A landscape scale conservation

management strategy for Swift Parrot breeding habitat currently being developed by the Tasmanian Government will need to address annual spatio-temporal variations in the distribution of nesting (including aggregations of nesting birds), the availability of nesting habitat relative to foraging habitat and their proximity to each other, and the long time scale required to replace suitable nesting trees. This will require the management or reservation of forest stands with old-growth characteristics across the breeding range and recognition that there may be several years between the use of any particular location by nesting Swift Parrots. Where hollow bearing forest is scarce relative to foraging habitat, retaining the existing hollow resource may be of particular importance.

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REFERENCES

Bennett, A.F., Lumsden, L.F., and Nicholls, A.O. (1994). Tree hollows in remnant woodlands, spatial and temporal patterns across the northern plains of Victoria, Australia. *Pacific Conservation Biology* **1**, 222-235.

Breslow, N.E., and Day, N.E. (1980). Statistical Models in Cancer Research. In: The Analysis of Case Control Studies. Vol. 1. (IARC Scientific Publications: Lyon)

Brereton, R. (1997). Management Prescriptions for the Swift Parrot in Production Forests. Report to the Tasmanian RFA Environment and Heritage Technical Committee.

Brereton, R., Mallick, S.A., and Kennedy, S.J. (2004). Foraging preferences of Swift Parrot on Tasmanian Blue-gum: tree size, flowering frequency and flowering intensity. *Emu* **104**, 377-383.

Brown, P.B. (1989). The Swift Parrot *Lathamus discolor*: A report on its ecology, distribution and status, including management considerations. Report to the Department of Lands Parks and Wildlife.

Commonwealth of Australia and State of Tasmania (1996). Tasmanian-Commonwealth Regional Forest Agreement. Environment and Heritage Report Vol. 1. Tasmanian Public Land Use Commission, Hobart.

Commonwealth of Australia and State of Tasmania (1997). Tasmanian Regional Forest Agreement. An agreement between The Commonwealth of Australia and The State of Tasmania.

Garnett, S.T., and Crowley, G.M. (2000). The Action Plan for Australian Birds. (Environment Australia: Canberra)

Gibbons, P., and Lindenmayer, D.B. (2002). Tree Hollows and Wildlife Conservation in Australia. (CSIRO Publishing: Melbourne)

Harper, M.J., McCarthy, M.A., and Ree, R. van der (2005). The abundance of hollow-bearing trees in urban dry sclerophyll forest and the effect of wind on hollow development. *Biological Conservation* **122**, 181-192.

Harris, S., and Kitchener, A. (2005). From Forest to Fjaeldmark: Descriptions of Tasmania's Vegetation. (Department of Primary Industries and Water, Printing Authority of Tasmania: Hobart)

Inions, G.B., Tanton, M.T., and Davey, S.M. (1989). Effect of fire on the availability of hollows in trees used by Common Brushtail Possum, *Trichosurus vulpecula* Kerr, 1793, and the Ringtail Possum *Pseudocheirus peregrinus* Boddaerts, 1785. *Australian Wildlife Research* **16**, 449-458.

Jackson, J. and Munks, S. (1998). Threatened fauna manual for production forests in Tasmania. Revised Edition. Forest Practices Board, Tasmania.

Jacobs, M.R. (1955). *Growth Habits of the Eucalypts*. Forest Timber Bureau Australia, Canberra.

Koch, A. J., Driscoll, D. A., and Kirkpatrick, J. B. (2008). Estimating the accuracy of tree ageing methods in mature *Eucalyptus obliqua* forest, Tasmania. *Australian Forestry* **71**, 147-159.

Lindenmayer, D.B., Cunningham, R.B., Pope, M.L., Gibbons, P., and Donnelly, C.F. (2000). Cavity sizes and types in Australian eucalypts from wet and dry forest types – a simple of rule of thumb for estimating size and number of cavities. *Forest Ecology and Management* **137**, 139-150.

Mac Nally, R., and McGoldrick, J.M. (1997). Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology* **28**, 171-183.

Mallick, S., James, D., Brereton, R., and Plowright, S. (2004). Blue-gums *Eucalyptus globulus* in north-west Tasmania: an important food resource for the endangered Swift Parrot *Lathamus discolor. Victorian Naturalist* **101**, 36-46.

Manning, A.D., Lindenmayer, D.B., and Barry, S.C. (2004). The conservation implications of bird reproduction in the agricultural "matrix": a case study of the vulnerable superb parrot of south-eastern Australia. *Biological Conservation* **120**, 363-374.

Mawson, P.R., and Long, J.L. (1994). Size and age parameters of nest trees used by four species of parrot and one Species of cockatoo in south-west Australia. *Emu* **94**, 149-155.

Munks, S., Richards, K., Meggs, J., and Brereton, R. (2004). The importance of adaptive management in 'off-reserve' conservation for forest fauna: implementing, monitoring and upgrading Swift Parrot *Lathamus discolor* conservation measures in Tasmania. In 'Conservation of Australia's Forest Fauna (second edition)' (Ed. D. Lunney) pp. 688-698. (Royal Zoological Society of New South Wales: Mosman, NSW.)

Saunders, D.A., Smith, G.T., and Rowley, I. (1982). The Availability and Dimensions of Tree Hollows that Provide Nest Sites for Cockatoos (Psittaciformes) in Western Australia. *Australian Wildlife Research* **9**, 541-556.

Stoneman, G.L., Rayner, M.E., and Bradshaw, F.J. (1997). Size and age parameters of nest trees used by four species of parrot and one species of cockatoo in south-west Australia: Critique. *Emu* **97**, 94-96.

Swift Parrot Recovery Team (2001). Swift Parrot Recovery Plan. Department of Primary Industries Water and Environment, Hobart.

Tilyard, P., and Potts, B. (2003). Flowering phenology of *Eucalyptus globulus* in Swift Parrot habitat in eastern Tasmania. Cooperative Research Centre for Sustainable Production Forestry, University of Tasmania. A Report to the Nature Conservation Branch.

van der Ree, R., Bennett, A.F., and Soderquist, T.R. (2006). Nest-tree selection by the threatened brush-tailed phascogale *(Phascogale tapoatafa)* (Marsupialia: Dasyuridae) in a highly fragmented agricultural landscape. *Wildlife Research* **33**, 113-119.

Williams, K., and Potts, B.M. (1996). The natural distribution of *Eucalyptus* species in Tasmania. *Tasforests* **8**, 39-164.

CHAPTER 3: Location matters: using spatially explicit occupancy models to predict the distribution of a highly mobile, endangered swift parrot.

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ABSTRACT

Occupancy modelling using data collected by repeatedly sampling sites is a common approach utilised by land managers to understand species distributions and trends. Two important factors that can complicate interpretation of these models are imperfect detection and spatial autocorrelation. We examine the effect of these potential errors using a multi-year data set on the distribution of the migratory and endangered swift parrot (*Lathamus discolor*). We simultaneously account for these effects by extending a zero-inflated Binomial (ZIB) framework to allow the inclusion of semiparametric, smooth spatial terms into both the occupancy and detection component of the model, in a maximum likelihood framework easily implemented in common software. This approach also has the advantage of relatively straightforward model selection procedures. We show that occupancy and detectability were strongly linked to food availability, but the strength of this relationship varied annually. Explicitly recognizing spatial variability through the inclusion of semiparametric spatially smooth terms in the ZIBs significantly improved models in all years, and we suggest this predictor is an effective proxy for unmeasured environmental covariates or conspecific attraction. Importantly, the spatially explicit ZIBs predicted fewer occupied sites in more defined areas compared to non-spatial ZIBs. Given the importance of predicted distributions

in land management, habitat protection and conservation of swift parrots, these models serve as an important tool in understanding and describing their ecology. Our results also reinforce the need for designing surveys that capture the underlying spatial structure of an ecosystem, especially when studying mobile aggregating species.

INTRODUCTION

Effective population monitoring is fundamental to threatened species management and conservation planning (Martin et al., 2007; Sanderson et al., 2006). The importance of developing effective monitoring designs and analytical approaches has generated considerable discussion (Reynolds et al., 2011; Rhodes and Jonzén, 2011; Wintle et al., 2010), particularly regarding the need to identify and account for sources of error. When the results of monitoring identify the need for management responses that are contentious, expensive or impact on industry, accounting for error becomes especially important (Martin et al., 2007).

Highly mobile, rare or cryptic species can be difficult and expensive to monitor. Because resources are often limited, collecting detection/non-detection data from a sample of sites to be analysed within an occupancy-modelling framework is a popular approach among land management agencies (Kéry et al., 2013). Consequently, occupancy models and the relationship between occupancy and abundance, have been used extensively to estimate species density, distributions and habitat associations (e.g. Gaston et al., 2000; Hui et al., 2006). Estimating and accounting for false negative error rates or detection probability is fundamental to improving the reliability of occupancy models (MacKenzie et al., 2002; Martin et al., 2005; Royle and Nichols, 2003; Tyre et al., 2003; Wintle et al., 2004). The most

common approach involves repeatedly sampling sites to estimate detection probability *p*, defined as the probability a species will be detected in a single site visit given that it occupies that site (MacKenzie et al., 2002). The detection process is commonly influenced by the behaviour and abundance of the target species (Gu and Swihart, 2004; McCarthy et al., 2013; Wintle et al., 2010), and if there is spatial or temporal heterogeneity in *p*, establishing its relationships with environmental variables can reduce bias in parameter estimators and improve sampling strategies (e.g. Bailey et al., 2004; Gibson, 2011; Lahoz-Monfort et al., 2014).

Errors in interpreting ecological relationships can also arise if spatial autocorrelation (SAC) is ignored, or not accounted for in the distribution of the target species (Dormann, 2007; Hawkins, 2012; Legendre, 1993). Generally, SAC originates from either an autocorrelated environment (i.e. where nearby locations are more similar than more distant ones) or through processes like conspecific attraction and limited dispersal ability of the target species (Lichstein et al., 2002). Importantly, recognition and analysis of SAC can provide insights into ecological processes that may otherwise be overlooked (Bini et al., 2009; Hawkins, 2012) and the effect of spatial structure has been recognised as an important component in modelling the occupancy-abundance relationship (Hui et al., 2006).

Recently, considerable attention has focused on improving statistical methods to account for either SAC or imperfect detection; however, relatively few studies have formally accounted for these processes simultaneously (but see Aing et al., 2011; Bled et al., 2011; Johnson et al., 2013; Royle et al., 2007). Some studies have accounted for spatial correlation in discrete spatial domains (Johnson et al., 2013; Royle et al., 2007; Wintle and Bardos, 2006), while

others have focused on the detection process in transect based or cluster sampling designs (Aing et al., 2011; Guillera-Arroita et al., 2010; Guillera-Arroita et al., 2012; Hines et al., 2010). Other approaches model spatial variability through the inclusion of spatially correlated random fields (Diggle et al., 1998; Post van den Burg et al., 2011). Most of these studies, and other occupancy models that contain autocorrelation structure adopt a hierarchical Bayesian perspective (see also Gardner et al., 2010; Hoeting et al., 2000; Sargeant et al, 2005).

In this study, we use the endangered swift parrot (*Lathamus discolor*) to illustrate the importance of accounting for SAC and detection when modelling the distribution of mobile, cryptic and threatened species. Swift parrots are a migratory nectarivorous species seriously threatened by anthropogenic habitat loss throughout their range (Higgins, 1999). Their breeding range is restricted to the island of Tasmania, Australia, where they nest in tree hollows and rely on the erratic flowering of the Tasmanian blue gum (*Eucalyptus globulus* subsp. *globulus*) and black gum (*Eucalyptus ovata*) for food (Webb et al., 2012). However, there are few empirical data that quantify the relationship between nectarivores and flowering at macroecological scales. The very specific nesting and food requirements of the swift parrot, and the need for hollows and flowering to occur in the same area, make the species highly vulnerable to the effects of continuing habitat degradation and loss (Webb et al., 2012).

A key question for land managers is: how much habitat needs to be protected to conserve the species? Approximately one-third of the swift parrots potential breeding habitat is afforded varying levels of protection through the Comprehensive, Adequate and Representative (CAR) Reserve System (see Commonwealth of Australia, 1992). However, conservation (or

protection) of non-reserved land (e.g. private land, production forest) that contains breeding habitat is highly contentious (Allchin et al., 2013) and can have serious economic implications for stakeholders. In this context, the relative importance of a particular area to swift parrots is often heavily scrutinised, especially where information is limited. Accurate, annual spatiotemporal information on the distribution of swift parrots, and the availability of their nesting and feeding habitat, is required to identify ecologically relevant spatial scales of management, prioritise key sites or regions, develop and inform off-reserve management actions, and set spatially explicit thresholds for habitat loss.

Given the dependence of swift parrots on flower for food, its use as a key explanatory variable was a logical starting point for our analyses. However, it is likely that other environmental or behavioural factors also influence occupancy and detection. From a logistical or economic perspective, it is often difficult to identify or measure these factors. We hypothesised that explicitly incorporating a smoothed spatial covariate in the occupancy and/or detectability component of zero-inflated Binomial models (ZIB) in a generalised additive model (GAM) framework, should help explain a large proportion of the variation due to these unknown or unmeasured factors. Our approach models the autocorrelation through smoothed functions of spatial coordinates where space is viewed as inherently continuous. This is in contrast to approaches that discretize space into regions or sites, and model spatial correlation through correlated random effects defined over sites in a Bayesian hierarchical framework (e.g. Bled et al., 2011; Johnson et al., 2013 and references therein; Wintle and Bardos, 2006). Our approach is more similar to geostatistical models in which spatial variability is modelled as spatially correlated random fields (e.g. Diggle, 1998; Post van de Burg et al., 2011). However, by modelling spatial variability through smooth functions of spatial coordinates rather than correlated random fields, our models can be fitted

with standard maximum likelihood methods avoiding the need for complex Markov Chain Monte Carlo techniques.

Here we describe the design and implementation of a monitoring program, and associated analytical techniques, to better understand the spatial ecology of swift parrots and inform a landscape-scale conservation management strategy. We fitted Binomial models (with perfect detection), and zero-inflated Binomial models (that accounted for imperfect detection) with and without a smooth spatial covariate in GAM and generalised linear model (GLM) frameworks respectively, to test our hypothesis about the importance of spatial location. Using these models, we mapped the predicted distribution of swift parrots to illustrate dramatic spatiotemporal variation in their occurrence and detectability, while highlighting the importance of accounting for SAC. We also used simulated spatially structured data to form more generalized insights from our models.

METHODS

Study area and sampling regime

We sampled across the known breeding range of the swift parrot (broadly defined by the natural range of *E. globulus*), which is restricted to Tasmania and covers approximately 10 000 km^2 (Fig. A1, Webb et al., 2012). Swift parrot detection/non-detection data were collected by repeatedly sampling a number of distinct sites over a three-week period in October 2009-2012 (number of sites ranged from 771 to 1034). A site was defined as a 200 m radius around a fixed point and the number of site visits, across all years, ranged from one to eight with a mean of 2.4 (see Appendix A for detailed sampling protocols). Flowering intensity (0-4 scale) was also recorded during these visits. Minimizing the amount of time taken for each annual survey reduced the likelihood of changes in detectability and violation

of the assumption of closure, which is inherent in the models utilised (MacKenzie et al., 2006; Rota et al., 2009). A small subset of sites (n=16) from the north-west of Tasmania that were geographically distinct from the rest of the sites (Fig. A1) was not used in the analyses to reduce their disproportionate impact as spatial outliers.

Spatial structure

The degree of SAC in the data was assessed using correlograms (based on Moran's I– Tiefelsdorf, 2000) of detection/non-detection (0, 1) and flowering score (0, 1, 2, 3, 4) for each year using Spatial Analyses in Macroecology v4 (SAM, Rangel et al., 2010).

Model form

While recognising that a range of factors potentially influence the probability of occupancy (Ψ) and probability of detection (p) of swift parrots, we deliberately kept the models simple, restricting the covariates to just flower and a semiparametric, smooth spatial term. Flower is recognised as a key driver of avian nectarivore distribution (Mac Nally and McGoldrick, 1997) and we hypothesised that other unmeasured environmental or behavioural factors would be captured by the spatial covariate. We also used the odds ratio of the flower coefficient to quantify the strength of its effect in the models.

Two classes of models were considered, a simple Binomial, where we assume p to be perfect and a ZIB, which accounts for imperfect detection. For the simple Binomial (Equation 1), y_i

is a binary indicator that is 1 if the target species was detected on any visit to site *i*, and 0 otherwise.

$y_i \sim \text{Binomial}(1, \Psi_i)$ Eq. 1.

Here Ψ_i is the probability that the target species is present at site *i* (assuming perfect detection), and is a function of the covariates.

The second class of models (ZIBs) assume that any site is either continuously occupied or unoccupied during the survey period, but detection is imperfect (but constant across the survey period). Hence, if the site is occupied, there is no guarantee the target species will be detected on any individual visit, and the observed detections are modeled with a zero-inflated Binomial distribution (Hall 2000) (Equations 2a, b). In this case

$y_i \sim \text{Binomial}(n_i, z_i p_i)$ Eq 2a

$z_i \sim \text{Binomial}(1, \Psi_i)$ Eq. 2b

where now y_i represents the number of times the target species was detected in n_i visits to the site. z_i is a latent binary variable that indicates whether a site is truly occupied. Here, $z_i = 1$ if the site is occupied and $z_i = 0$ if the site is unoccupied, and so $y_i > 0$ implies $z_i = 1$ and $z_i = 0$ implies $y_i = 0$. Again, Ψ_i is the probability that site *i* is occupied, and p_i is the conditional probability that a detection will occur on any single occasion if the site is occupied (assuming that detections occur independently). In turn, the probabilities of Ψ_i and p_i can be related to site-specific covariates.

Model fitting

Data were analysed for each year separately. First, we fitted the standard Binomial model using logistic regression with Ψ as a function of the variable *flower* (*F*) (Equation 3) using library glm in R (R Development Core Team, 2013). In vector notation

$$\log(\Psi/1\text{-}\Psi) = \alpha + \beta_1 F \qquad \text{Eq. 3}$$

where Ψ is now the vector of probabilities that the target species is present at the sites, and *F* the vector of flower scores.

Autologistic models (Augustin et al., 1996) were then fitted, again with Ψ as a function of *flower* but with the addition of a spatial autocovariate (calculated using the default settings in SAM v4.0, logistic regression module) (Equation 4). Again, in vector notation

$$\log(\Psi/1\text{-}\Psi) = \alpha + \beta_1 F + cWy \qquad \text{Eq. 4}$$

Here *Wy* represents the spatial autoregressive term, where *y* is now a binary vector indicating the presence or absence of the target species at each of the sites, *W* is the spatial relationship matrix that reflects the relation between each site and its neighbours, and *c* is the autoregressive parameter.

As a third alternative, we used the mgcv library in R (Wood, 2004) to fit a Binomial GAM that modelled Ψ as a function of *flower* and a smooth function *s*(*lat*, *lon*) of location covariates (Equation 5). We allowed the mgcv package to select the appropriate level of smoothing.

$$\log(\Psi/1\text{-}\Psi) = \alpha + \beta_1 F + s(lat,lon) \qquad \text{Eq. 5}$$

To examine the effect of adding a spatial covariate, we also compared the amount of SAC remaining in the residuals of each model fitted. AIC scores were used to rank the overall fit of the models (Burham and Anderson, 2002).

Three approaches were used to fit the ZIBs. First, data were analysed separately for each year in program PRESENCE (Hines, 2012), where both Ψ and p are a function of *flower*. In principle, the ZIBs can also be fitted using VGAM package in R (Yee et al., 2010) and this package was used to fit ZIBs with *flower* as the only predictor. However, extensive tests on simulated data found VGAM ZIBs to be unreliable when a spatial covariate was added. Specifically, they would not converge with a spatial covariate term (i.e. the ZIB equivalent of Equation 5) and this approach was not pursued. Instead, ZIBs with the smooth location covariate were fitted using the EM Algorithm (Dempster et al., 1977) implemented in R (R Core Development Team, 2013). The EM Algorithm is an iterative procedure for deriving maximum likelihood estimates in the presence of missing data. The ZIB model can be fitted with the EM algorithm by treating the latent z_i as missing data. Starting from an initial estimate, the EM algorithm is an iterative two-step process that generates a sequence of estimates guaranteed to converge to the maximum likelihood estimate (see Appendix B for full details). While, circumstances exist where the ZIB model is degenerate, (e.g. with only one visit it is not possible to separate detection from occupancy); here we assume that sites are sampled sufficiently often that the likelihood has a unique maximum. To the best of our knowledge, this is the first successful implementation of ZIB occupancy models that incorporate a smoothed spatial covariate in a GAM framework using empirical ecological data. AICs were again used to compare the fit of all ZIBs, with the exception of the PRESENCE models, which were not comparable to other models due to differences in the way maximum likelihood is computed.

Predictions of occupancy and detectability

To compare predictions among all models, we generated spatially explicit estimates for Ψ (simple Binomial models and ZIBs) and p (ZIBs only). To better visualize the results, we interpolated the predictions at ecologically relevant scales (kriging with 0.02° pixel size, maximum of 50 neighbours and neighbor search radius of 0.05° (~5 km)) across the study area (implemented in Manifold Systems Professional V8 GIS software).

Simulations

Although we demonstrated that the EM algorithm could be used to fit ZIBs, it was unclear whether these models were identifiable when the probabilities of Ψ and p are related to site specific covariates, or whether spatial variability in p will be confounded with variability in Ψ. If the two components cannot be clearly distinguished, there may be no value in fitting models that explicitly represent both p and Ψ. To address these issues, we first used simulated data to test if the model was indeed identifiable, and that variability in p could be distinguished from variability in Ψ. Second, we qualitatively compared the fit of the ZIBs with a presence-absence (or detection/non-detection) Binomial model (directly analogous to our simple GAMs).

We simulated data by generating N random sites distributed uniformly on the [0,1] x [0, 1] square. Predictors were calculated for each site and used to construct the probability of occupancy at a site, and the probability of detecting the target species if the site is occupied. In these simulations, at least one visit was conducted at every site, and the number of

additional visits was assumed to be Poisson distributed. Three of the predictors used were smooth functions of space, with two being sinusoids and the third a plane while the remaining two predictors were uniform random fields. Full details of the simulations are provided in Appendix C. The R code used to implement the EM Algorithm and the simulations is provided in Appendix D.

RESULTS

Overview

The frequency of flower scores and sites where swift parrots were detected are summarised in Table 1. Naïve occupancy (i.e. proportion of sites where swift parrots were detected) over the four years ranged from 0.094 – 0.187. Flowering conditions varied between years (both in intensity and geographically), being generally very poor with localised flowering in 2009 (mainly in the south-eastern region), a mast flowering event in 2010 (again highest in the south-east), localised flowering in 2011(north-eastern region) and again in 2012 (mainly in the south) (Fig. 1).

Table 1. Summary of the frequency of flower score (0, 1, 2, 3, 4) and the number of sites where swift parrots were detected, 2009-2012.

Flower score	2009	sites birds detected	2010	sites birds detected	2011	sites birds detected	2012	sites birds detected
0	586	16	373	28	787	35	621	29
1	70	3	149	29	83	20	135	16
2	61	16	138	35	85	33	103	32
3	45	31	152	54	46	23	100	54
4	9	6	38	13	33	26	27	21

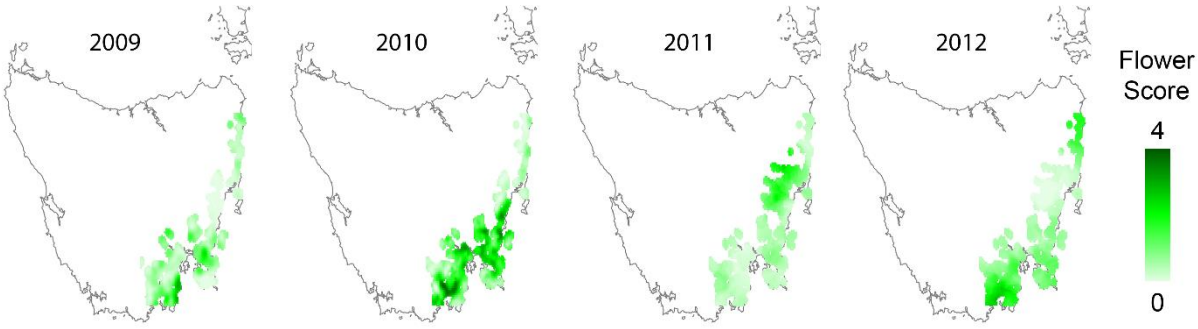

Figure 1. Interpolated distribution of flowering over the swift parrot breeding range in each year. Flowering was scored on a 0-4 scale, and smoothed using kriging with a 0.02° cell size, 50 neighbours in a maximum 0.05° radius.

Spatial structure

Correlograms indicated significant SAC in swift parrot detection/non-detection and *Eucalyptus* flowering in all years (Fig. 2a-d). Flowering was significantly spatially autocorrelated (Morans I test) out to a distance of 25-51 km and varied between years. In 2009, 2011 and a slightly lesser extent in 2012, the SAC in *detection* followed a similar pattern to that of *flower*, and was spatially autocorrelated out to approximately 30-35 km in those years; however, in 2010 *detection* was spatially autocorrelated out to a distance of over 40 km with a less similar pattern to that of *flower* (Fig. 2).

Models assuming perfect detectability (p=1)

Not surprisingly, given the evidence for spatial structure in the data, all models improved (as indicated by lower AICs) when a spatial covariate was added. The best performing model in each year (where *p* was assumed to be perfect) was the Binomial GAM (Table 2, see also

Table A1a-d for all model coefficients and odds ratios). Models in 2010 showed the most improvement after the addition of the spatial covariate, which reflected the reduced spatial dependency on flowering in that year. Odds ratios also showed that *flower* was much less important as a predictor in 2010 compared to other years (Table 2).

Correlograms of the residuals showed that the inclusion of the spatial predictor in the GAM removed all significant, positive SAC (Fig. A2a-d). In 2009 and 2011 (when flowering was more sparse but locally concentrated), *flower* alone accounted for far more of the spatial structure in the residuals compared to 2010 (Moran's $I < 0.1$ in 2009 and 2011, and < 0.2 in 2012 compared to 0.4 in 2010 in the first distance class, Fig. A2).

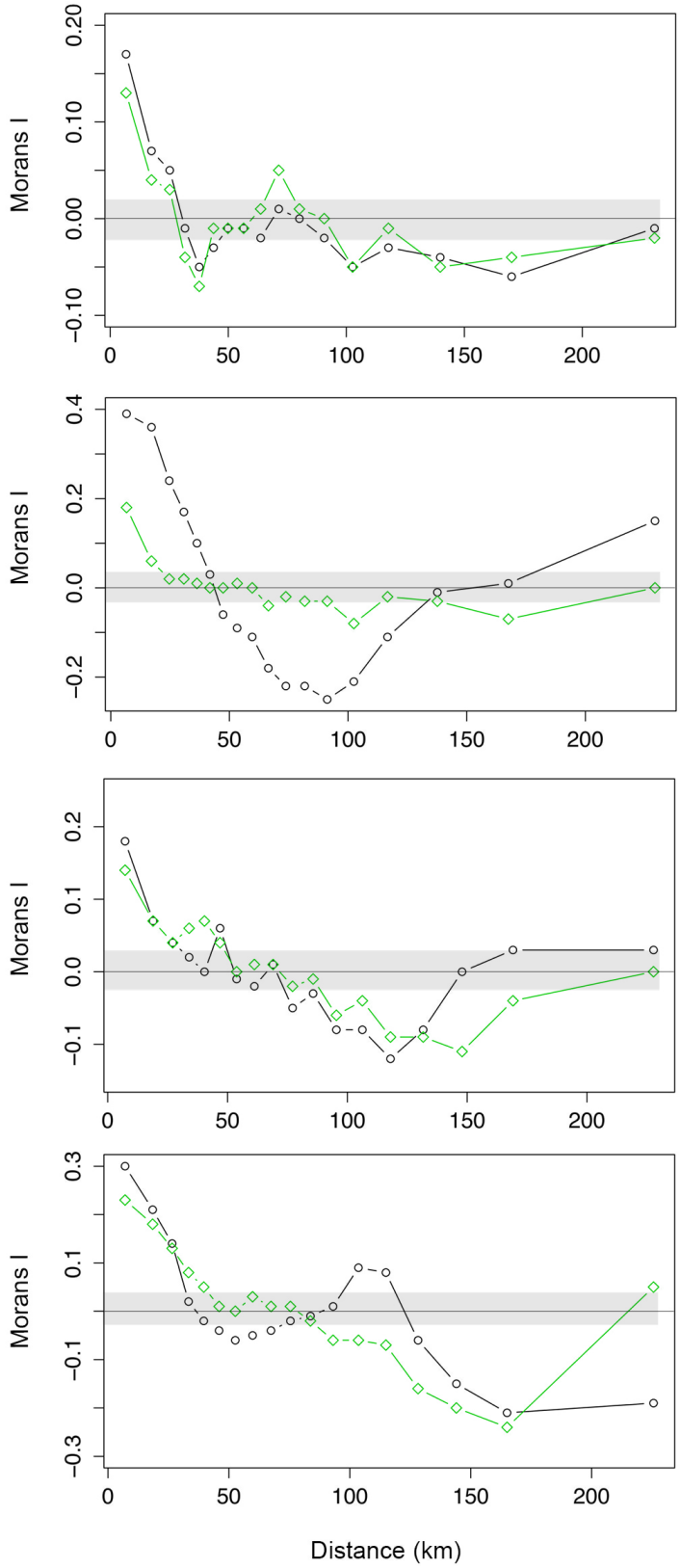

Figure 2. Spatial autocorrelation (Morans I) in swift parrot detection/non-detection (black circles) and corresponding flower data (green diamonds) across the breeding range, for years 2009–2012. Shaded areas represent non-significant spatial autocorrelation ($p<0.05$) as indicated by the Morans I test.

Zero-inflated Binomial models

Five ZIBs were fitted in each year (Tables 2 and A1). According to AICs, the VGAM and EM Algorithm models without spatial covariates were almost identical in their fit and all non-spatial ZIBs had very similar coefficients (Table A1). Models with a spatial covariate in either the Ψ and/or p component (i.e. GAM-ZIB framework) were better than those without the spatial covariate (i.e. GLM-ZIB framework) in all years (Table 2). The standard errors computed through the EM algorithm are unreliable, and in general it is difficult to relate these to the true standard errors. Louis (1982) shows that the complete data information matrix required to compute the true standard errors can be expressed as the observed data information matrix adjusted for the information missing due to the missing observations (in our case, the true site occupancies). In principle, this result can be leveraged to estimate the true standard errors, but in practice this not a simple computation, and we could not see how to implement this in the general case. Therefore we have not included them in Table A1.

Odds ratios were again used to illustrate the relative importance of *flower* in the models. Odds ratios indicated that *flower* was an important predictor in modelling both Ψ *and* p in 2012, but had less influence on both components in 2010 (Table 2). By contrast, there were more obvious differences in the relative importance of *flower* between the Ψ and p components in 2009 (minimal influence on Ψ, strong effect on p in the two best models) and 2011 (very strong effect on Ψ, little predictive power for p across all models).

Model predictions of Ψ and p

Predictions from the best simple GAMs (where p=1) all showed high probability of swift parrot presence in fairly discrete kernels (Fig. 3a). These areas differed among years, suggesting that swift parrots are not only flexible in their habitat utilisation, but also utilised much of the available habitat over time. While these predictions are useful for comparative purposes, from here on we focus more on models that account for imperfect detection.

The inclusion of the spatial predictor in the *p* component of the ZIB models highlighted considerably more heterogeneity in the detection process than that observed in the models without spatial covariates (mean range of *p* in spatial models= 0 - 0.89 *cf*. 0.22 – 0.64 in non-spatial models, Fig. A3, A4a, b). The low estimates of *p* in the spatial models were generally at sites geographically disjunct from clusters of sites where birds were detected (i.e. the informative sites for estimating *p*). This also resulted in markedly different Ψ predictions, with generally high probabilities in a relatively narrow range (mean range of Ψ: 0.58 – 0.99; Fig. A4c). The high predictions over the narrow range can largely be attributed to uncertainty surrounding estimates at many sites where *p* was very low, which in turn is likely related to the number of visits (see also Appendix C - p6 and Fig. 13). Low detectability also confounded realistic occupancy predictions in the models that included a spatial covariate in both components (Fig. A5a).

Although AIC scores suggested that models with the spatial component in detection often performed better (Table 2), the resulting Ψ predictions were clearly unsatisfactory (Figs. A4c, A5a). For this reason we focus on Ψ estimates from ZIB models with the spatial covariate only in the Ψ component. Non-spatial ZIBs showed more diffuse predictions (Fig. 3b), and

the range of predictions was typically smaller than those models with a spatial predictor in the Ψ component (mean Ψ range: 0.13 - 0.80 *cf*. 0 – 0.97, Fig A6). Direct comparisons of the predictions indicate non-spatial models (Fig. 3b) generally over and underestimate Ψ compared to models with a spatial covariate (Fig. 3c).

ZIBs with the spatial covariate in the Ψ component provided similar predictions to the simple Binomial GAMs, with concentrated kernels of high probability and areas of low probability over much of the breeding range (Fig. 3a, c). Despite the apparent visual similarities of the predictions from the two models, pixel-by-pixel comparisons clearly highlighted the influence of p on Ψ predictions (Fig. A7). For example, in 2010 there was close agreement between Ψ estimates (Fig A7), with relatively constant p across the range (Fig. A8). By contrast, in 2009 there was much less agreement in predictions between the two models (Fig. A7). This year differed from others in that a relatively high proportion of sites were only visited once (~50%), and these had very low estimates of p (median < 0.1 – Figs A3a, A8).

Table 2. Form of models fitted and corresponding AIC values where Ψ =probability of occurrence, p = probability of detection and bracketed terms represent the covariates included in the models. Flower = score 1-4; s(lat,lon) = bivariate smooth location term. Note that the AICs of the simple models and the AICs of the zero-inflated Binomial models (ZIBs) are not comparable; AICs for PRESENCE model are not comparable with those fitted with the EM Algorithm and AICs are not comparable across years. † denotes best models for p=1 . * denotes best ZIB. Odds ratios indicating the relative strength of the variable *flower* are shown in brackets after the AIC values. 1. Rangel et al., (2010); 2. Wood, (2004); 3. Hines, (2012); 4. Yee et al., (2010); 5. Implementation developed in this study (see Appendix B for details)

Model	**Implementation**	**AIC (2009)**	**AIC (2010)**	**AIC (2011)**	**AIC (2012)**
Ψ(*flower*) .p(1)	SAM[1]	288	756	571	631.5
Ψ(*flower+cW*) .p(1)	SAM[1]	251	509	458	488
Ψ(*flower+s(lat,lon)*) .p(1)	R-package: mgcv[2]	237 (5.0)†	507 (1.6)†	447 (3.0)†	473 (2.8)†
Zero-inflated Binomial models					
Ψ(*flower*).p(*flower*)	PRESENCE[3]	689	1306	1006	1003
Ψ(*flower*).p(*flower*)	R-package: VGAM[4]	did not converge	1035	782	832
Ψ(*flower*).p(*flower*)	EM Algorithm[5]	448 (2.8, 2.5)	1035 (1.8, 1.1)	782 (3.2, 1.4)	832 (2.2, 2.0)
Ψ(*flower*).p(*flower* + *s*(*lat,lon*))	EM Algorithm[5]	400 (1.5, 4.2)	807 (1.5, 1.4)	672 (5.9, 1.5)	683* (3.4, 2.2)
Ψ(*flower* + *s(lat,lon)*)).p(*flower*)	EM Algorithm[5]	440 (2.6, 2.4)	808 (1.5, 1.1)	665* (6.7, 1.3)	694 (2.0, 1.9)
Ψ(*flower* + *s(lat,lon)*).p(*flower+s(lat,lon)*)	EM Algorithm[5]	390* (1.9, 4.5)	783* (2.0, 1.4)	671 (7.2, 1.3)	686 (2.5, 2.4)

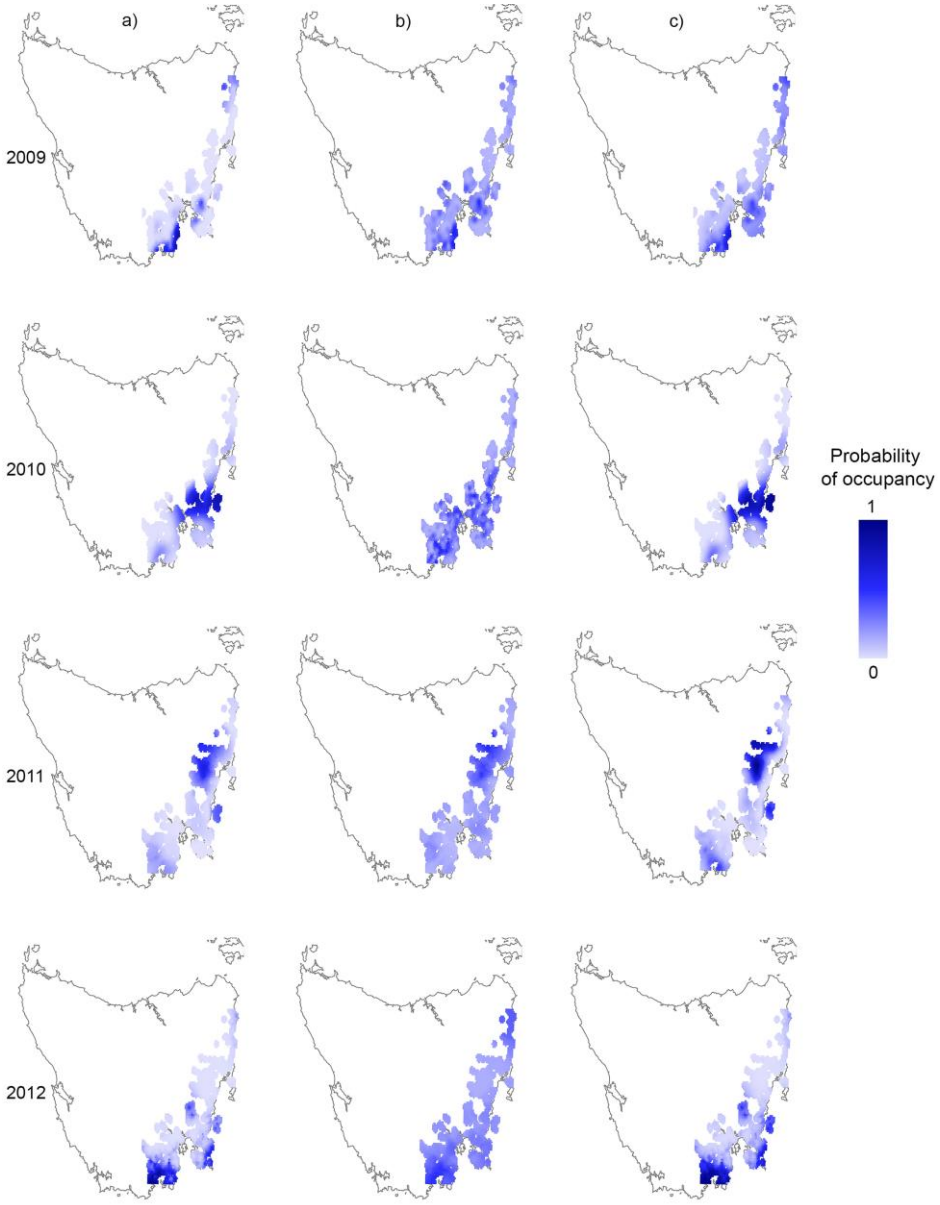

Figure 3. Prediction maps of swift parrot occupancy 2009-2012, showing: a) simple generalised additive models; b) standard zero-inflated Binomial models with generalized linear models and no spatial covariate; and c) zero-inflated Binomial models with the spatial covariate in the occupancy component only. Predictions are smoothed from point data using kriging with a 0.02° cell size, 50 neighbours in a maximum 0.05° radius.

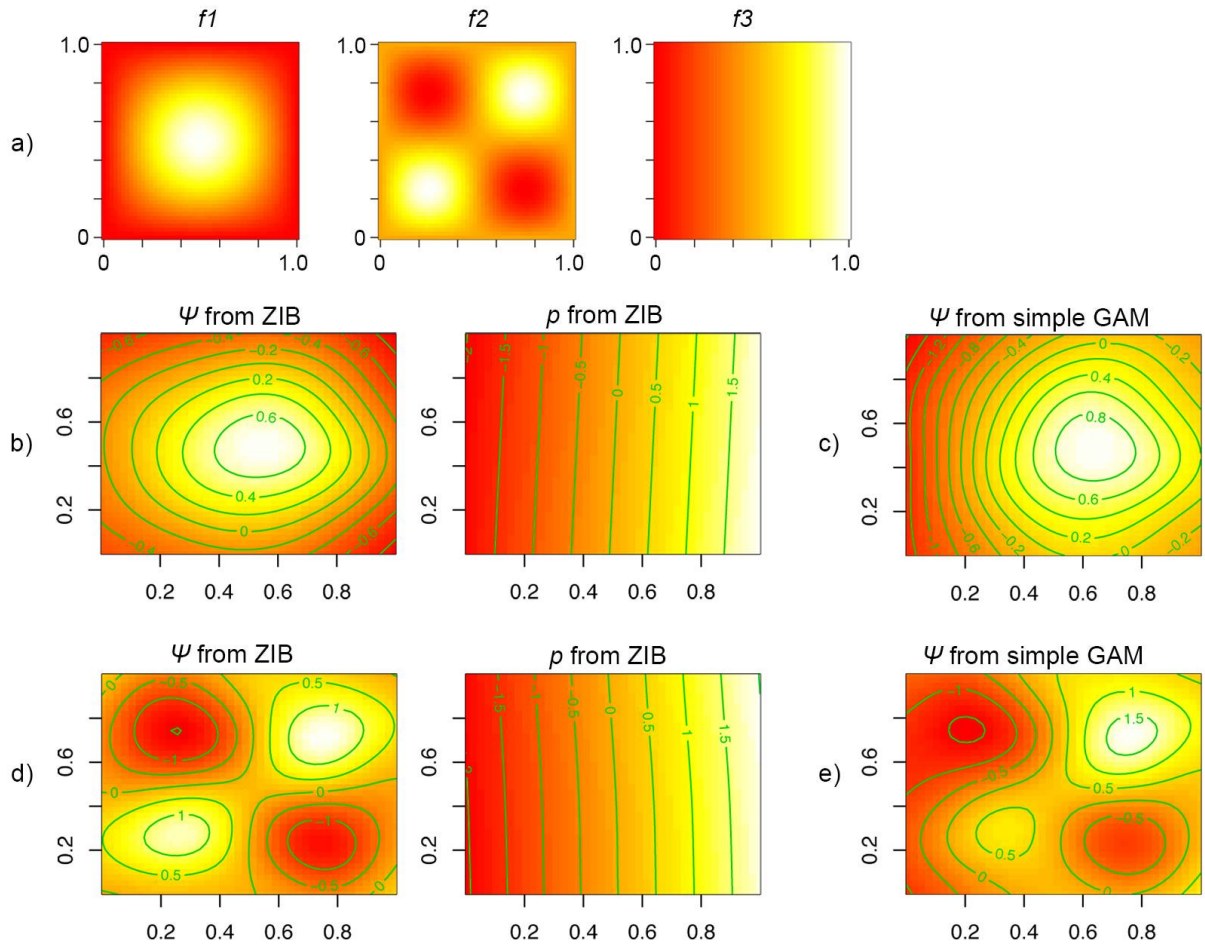

Figure 4. Fitted smooths from the GAM simulations when detectability varies across the domain. a) the structure of the three spatially smooth predictors; b) zero-inflated Binomial model (ZIB) - occupancy (Ψ) spatial structure from f_1 and detectability (p) spatial structure from f_3; c) simple Binomial generalized additive mode (GAM) – occupancy from model including f_1 and f_3; d) zero-inflated Binomial model - Ψ spatial structure from f_2 and p spatial structure from f_3; e) simple Binomial GAM – occupancy from model including f_2 and f_3 (see Appendix C for further details and all simulated model comparisons).

Simulations

The simulations showed that when p was constant, both the zero-inflated and simple Binomial models detect the factors influencing Ψ, including spatial structure (Appendix C).

However, consistent with the empirical results reported above, when p varies, the ZIB is able to separate factors influencing p and Ψ (Fig. 4). By contrast, the simple GAMs (where p=1) confound the factors influencing p with those influencing Ψ and conflate these estimates (Fig. 4, Appendix C). For example, if we take several forms of clear spatial structure (Fig. 4a) and incorporate them into our simulated models, the linear trend (f_3 in Fig. 4a) in p across the domain is not reflected in the fitted smooth of the Ψ component of the ZIB (Fig. 4b).

However, estimates of Ψ from the simple GAM suggest that the latter both overestimates and underestimates Ψ across much of the space (Fig. 4c). Similarly, in Fig. 4d, the spatial trends in both Ψ and p are distinguished much more accurately in the ZIB and while Ψ estimates from the simple GAM do capture some of the spatial structure, they are clearly confounded by the factors influencing p as well. For more details on the model simulations and associated results see Appendix C.

DISCUSSION

Our study demonstrates that complex and spatiotemporally variable interactions between a difficult to study species and their food source can be effectively monitored and modelled to inform conservation management. Through the use of a smoothed spatial covariate in occupancy models, we provide another tool that can be used to address common challenges facing survey design and associated distributional analyses that typically hamper monitoring and conservation efforts for mobile, aggregating animal populations. Untangling the processes influencing detection and occupancy is important for avoiding misleading inferences, especially as such processes are often inextricably linked, with some clearly influencing both parameters while others may only affect one or the other. We highlight the

importance of accounting for spatial autocorrelation, not only for modelling animal occurrence, but also for understanding the detection process. Furthermore, the potential of more flexible models (such as the GAM based models we utilise here) has been recognised, and while it has been suggested that they may produce superior occupancy models, they had yet to be implemented successfully with empirical data (Martin and Fahrig, 2012).

Across all models, the importance of *flower* as a predictor increased as its availability decreased (e.g. 2009). By contrast, the importance of site location (i.e. the smoothed spatial covariate) increased with the availability of flowering (e.g. 2010), suggesting that other processes also influenced swift parrot distribution. The empirical observations were supported by the simulations, which demonstrated that incorporating the spatial covariate into ZIBs allowed the spatial structure present in both Ψ and p to be identified, whereas the simple Binomial GAMs confound the factors influencing Ψ and p. When spatial structure is present (as is typically the case for mobile, aggregating species), ignoring spatial location in the absence of other explanatory variables when modelling Ψ or p can mislead inferences. In the swift parrot models the importance of the spatial covariate varied between Ψ and p in each year. However, the inclusion of the spatial covariate in the p component of the ZIB produced very low estimates (e.g. <0.01) for sites that were geographically distinct from the informative sites (i.e. sites where birds were detected), which in turn resulted in unreliable estimates of Ψ for those sites. Typically this can be attributed to too few repeated visits (e.g. Guillera-Arroita et al., 2010), but can also be related to the type of model fitted (and the interactions between the occupancy and detectability component).

Notwithstanding these limitations, the spatially explicit estimates of detectability may provide important insights into interpreting spatial variation in swift parrot population density. When Ψ and p both increase with a covariate, as they do in our study with *flower*, this can indicate the abundance of the target species is responding to the covariate (Yackulic et al., 2013). Such a trend would suggest a positive abundance-occupancy and/or abundance-detectability relationship (Gaston et al., 2000; McCarthy et al., 2013). We argue that much of the heterogeneity in both Ψ and p in this study originates from variations in the abundance of swift parrots over multiple spatial scales (i.e. from site to landscape scales). Here, the detection process is likely influenced by (i) increased calling frequency as abundance increases at the site level, and (ii) increased abundance of birds in the landscape surrounding a site, increasing the probability of a bird being present and therefore detected at a site when it is sampled. These complex interactions highlight the importance of studying the ecological mechanisms driving the occupancy/detection processes in spatially structured systems, and understanding the response of aggregated species distributions to the influence of environmental drivers at different spatial scales (Hui et al., 2010; Martin and Fahrig, 2012; Welsh et al., 2013).

The importance of testing and accounting for SAC will vary depending on the scale and level of aggregation of the target species and environmental predictors. The advantage of our approach (i.e. smoothed spatial location) is that it provides a more natural description of spatial structuring (or aggregation) because there is no requirement for *a priori* groupings of sites into clusters, transects or discrete spatial domains (e.g. Aing et al., 2011; Hines et al., 2010; Johnson et al., 2013), which can be arbitrary or ecologically irrelevant (Guillera-Arroita et al., 2011). Our methods also provide the potential to account for more sources of heterogeneity in Ψ or p, and improve understanding of bias in parameter estimators. Our

approach is likely to be particularly relevant to surveys conducted at large spatial scales in dynamic systems when few ecologically relevant covariates are available, or when the scale of effect of an environmental factor is unknown or varies across multiple temporal and spatial scales. For example, in this study *flower* is important at the site level (i.e. 200 m radius), but our predictions also suggest its effect operates at much larger spatial scales. Further, the scales of effect vary from year to year depending on overall flowering conditions.

While the geostatistical methods mentioned above also view space as continuous, our approach provides an alternative with the advantage of much simpler model selection procedures. We hope this ease of implementation and model assessment makes our method more accessible to land managers, which may not always have the statistical knowledge to tackle complex problems or the resources to implement more complex analytical techniques. While our implementation, using the EM Algorithm has the disadvantage of not providing standard errors around estimates; the improvement in the models, and consequent improvement of occupancy estimates, identify discrete defined areas of important habitat at ecologically relevant scales. On the whole, we think it better to utilise the advantages of more flexible, GAM based ZIBs (as noted by Martin and Fahrig, 2012), and suggest that in many cases, a better model with no standard errors is more informative than a weaker model with standard errors. While the EM Algorithm implementation does represent a compromise in this respect, it is very likely that future work will develop implementations that include estimates of uncertainty.

Often budgetary and logistic constraints may prevent adequate spatial replication to capture spatial structure and undertake multiple repeat visits. However, we show that devising a

sampling design that captures the underlying spatial structure of the study system can be just as important as addressing imperfect detection. Additionally, as recently noted by Johnson et al., (2013), exploiting SAC may reduce the need for many repeat visits because spatial dependence between sites compensates for the lack of temporal replication. However, it is a trade-off, and we recognise that repeat surveys will always decrease the likelihood of recording false absences. This study, together with other recent reviews, have highlighted the value of considering and utilising multiple statistical frameworks to better understand underlying ecological mechanisms, and to avoid misleading inferences (Martin and Fahrig, 2012; Welsh et al., 2013).

Implications for swift parrot conservation

Our study describes dramatic spatiotemporal variation in the swift parrot population driven by the distribution of *Eucalyptus* flowering. To our knowledge, this is the first population level study of a highly mobile nectarivore to describe macroecological patterns in distribution and demonstrate a spatial dependency on flowering. Understanding the variation in importance of the spatial covariate may provide insights into the mechanisms driving variations in the abundance of swift parrots. The SAC not explained by *flower* may be due to processes such as conspecific attraction or the omission of other unmeasured but ecologically important explanatory variables (e.g. availability of nesting sites or variations in the density of food trees). Similarly, the spatial covariate may explain larger scale effects, whereby site quality (as perceived by swift parrots) may also be dependent on flowering conditions at larger spatial scales than our site level measurement.

The spatially explicit models developed here represent a significant improvement on non-spatial models (as indicated by AICs) and the associated predictions of Ψ are over much smaller and more discrete areas. Improving models and associated predictions in this way not only reduces uncertainty about the species distribution, but also provides land managers with more confidence in making decisions that affect other stakeholders. Our findings are critical to informing these decisions because: (i) only a fraction of the breeding range appears suitable (and occupied) in most years (due to the co-occurrence of hollows and flowering), but that fraction varies considerably between years; (ii) we can identify focal regions for protection or restoration (see Fig. 3c), and provide robust quantitative thresholds (i.e. occupancy probability) on which to base these decisions; (iii) they allow an assessment of habitat availability to better inform the development of spatially explicit off-reserve conservation strategies and; (iv) we provide an analytical framework for understanding population level processes into the future (e.g. predation risk – see Stojanovic et al., in press) and the likely impacts of climate change on flowering. Most importantly, we clearly identify areas of the breeding range that need to be managed in a way that provides enough habitat for the majority of the population to breed and forage in a given year.

Our study was developed to tackle the challenges inherent in devising an effective and informed conservation strategy for the endangered swift parrot. Many other species behave in similar ways, but due to statistical and logistic challenges, rigorous monitoring of their movements and ecology across multiple spatial scales has not been possible (Newton, 2006). Our methods represent an effective tool for monitoring and modelling these difficult to study species, and form the basis of an accessible analytical framework to assist conservation managers in overcoming the barriers to collecting informative and reliable distributional data.

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SUPPORTING INFORMATION

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.05.017.

REFERENCES

Aing, C., Halls, S. Oken, K. Dobrow, R., Fieberg. J. 2011. A Bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated, sites. Journal of Applied Ecology 48, 1508-1517.

Allchin, R., Kirkpatrick, J., Kriwoken, L. 2013. On not protecting the parrot: Impact of conservation and planning legislation on an endangered species in Tasmania. Journal of Wildlife Law and Policy 16, 81-104.

Augustin, N. H., Mugglestone, M. A., Buckland, S. T. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33, 339-347.

Bailey, L. L., Simons, T. R., Pollock, K. H. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications 14, 692-702.

Bini, L. M., Diniz, J. A. F., Rangel, T., Akre, T. S. B., Albaladejo, R. G., Albuquerque, F. S., Aparicio, A., Araujo, M. B., Baselga, A., Beck, J., Bellocq, M. I., Bohning-Gaese, K., P. A. V. Borges, P. A. V., Castro-Parga, I., Chey, V. K., Chown, S. L., de Marco, P., Dobkin, D. S., Ferrer-Castan, D., Field, R., Filloy, J., Fleishman, E., Gomez, J. F., Hortal, J., Iverson, J. B., Kerr, J. T., Kissling, W. D., Kitching, I. J., Leon-Cortes, J. L., Lobo, J. M., Montoya, D., Morales-Castilla, I., Moreno, J. C., Oberdorff, T., Olalla-Tarraga, M. A., Pausas, J. G., Qian, H., Rahbek, C., Rodriguez, M. A., Rueda, M., Ruggiero, A., Sackmann, P., Sanders, N. J., Terribile, L. C., Vetaas, O. R., Hawkins, B. A.. 2009. Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. Ecography 32, 193-204.

Bled, F., Royle, J. A., Cam, E. 2011. Hierarchical modelling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. Ecological Applications 21, 290-302.

Burnham, K. P., Anderson, D. R. 2002. Model Selection and multi-model inference, Second Edition. Springer Verlag, New York.

Commonwealth of Australia. 1992. Joint ANZECC/MCFFA National Forest Policy Statement Implementation sub-committee (JANIS), Nationally Agreed Criteria for the establishment of a Comprehensive, Adequate and Representative Reserve System for forests in Australia, Canberra.

Dempster, A., Laird, N., Rdin, D. 1977. Maximum likelihood from incomplete data via the EM Algorithm. Journal of the Royal Statistical Society, Series B 39, 1-38.

Diggle, P. J., Tawn, J. A., Moyeed, R. A. 1998. Model-based geostatistics. Journal of the Royal Statistical Society 47, 299-350.

Dormann, C. F. 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Global Ecology and Biogeography 16, 129-138.

Gardner, C. L., Lawler, J. P., Hoef, J. M. V., Magoun, A. J.. 2010. Coarse-scale distribution surveys and occurrence probability modeling for wolverine in interior Alaska. Journal of Wildlife Management 74, 1894-1903.

Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M., Lawton, J. H. 2000. Abundance–occupancy relationships. Journal of Applied Ecology 37, 39-59.

Gibson, L. A. 2011. The importance of incorporating imperfect detection in biodiversity assessments: a case study of small mammals in an Australian region. Diversity and Distributions 17, 613-623.

Gu, W., Swihart, R. K.. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. Biological Conservation 116, 195-203.

Guillera-Arroita G., Morgan, B. J. T., Ridout, M. S., Linkie, M. 2011. Species occupancy modelling for detection data collected along a transect. Journal of Agricultural,

Biological and Environmental Statistics 3, 301-317

Guillera-Arroita, G., Ridout, M. S., Morgan B. J. T.. 2010. Design of occupancy studies with imperfect detection. Methods in Ecology and Evolution 1, 131 -139

Guillera-Arroita, G., Ridout, M. S., Morgan, B. J. T., Linkie, M. 2012. Models for species-detection data collected along transects in the presence of abundance-induced heterogeneity and clustering in the detection process. Methods in Ecology and Evolution 3, 358-367.

Hall, D. B. 2000. Zero-inflated Poisson and Binomial regression with random effects: a case study. Biometrics 56, 1030-1039.

Hawkins, B. A. 2012. Eight (and a half) deadly sins of spatial analysis. Journal of Biogeography 39, 1-9.

Higgins, P. J., editor. 1999. Handbook of Australian, New Zealand and Antarctic Birds. Oxford University Press, Melbourne.

Hines, J.E. 2012. PRESENCE 5.5 – Software to estimate patch occupancy and related parameters. USGS-PWRC. Available at: http://www.mbr-pwrc.usgs.gov/software/presence.html.

Hines, J. E., Nichols, J. D., Royle, J. A., MacKenzie, D. I., Gopalaswamy, A. M., Kumar, N. S., Karanth K. U. 2010. Tigers on trails: occupancy modeling for cluster sampling. Ecological Applications 20, 1456-1466.

Hoeting, J. A., Leecaster, M., Bowden D. 2000. An improved model for spatially correlated binary responses. Journal of Agricultural, Biological, and Environmental Statistics 5, 102-114.

Hui, C., McGeoch, M. A., Warren M. 2006. A spatially explicit approach to estimating species occupancy and spatial correlation. Journal of Animal Ecology 75, 140-147.

Hui, C., Veldtman, R., McGeoch, M. 2010. Measures, perceptions and scaling patterns of

aggregated species distributions. Ecography 33, 95-102.

Johnson, D. S., Donn, P. B., Hooten, M. B., Ray, J. C., Pond, B. A.. 2013. Spatial occupancy models for large data sets. Ecology 94, 801-808

Kéry, M., Guillera-Arroita, G., Lahoz-Monfort, J. J.. 2013. Analysing and mapping species range dynamics using occupancy models. Journal of Biogeography 40, 1463-1474.

Lahoz-Monfort, J.J., Guillera-Arroita, G., Wintle, B.A. (2014) Imperfect detection impacts the performance of species distribution models. Global Ecology and Biogeography 23, 504-515

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659-1673.

Lichstein, J. W., Simons, T. R., Shriner, S. A., and Franzreb, K. E. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs 72, 445-463.

Louis, T.A. 1982. Finding the observed information when using the EM Algorithm. Journal of the Royal Statistical Society B44, 226-233.

Mac Nally, R., McGoldrick, J. M. 1997. Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. Journal of Avian Biology 28, 171-183.

MacKenzie, D., Nichols, J., Lachman, G., Droege, S., Royle, J. A., Langtimm, C. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248-2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., Hines, J. E. 2006. Occupancy estimation and modelling: inferring patterns and dynamics of species occurrence. Elsevier, San Diego, California.

Martin, A. E., Fahrig, L. 2012. Measuring and selecting scales of effect for landscape

predictors in species-habitat models. Ecological Applications 22, 2277-2292

Martin, J., Kitchens, W. M., J. E. Hines. 2007. Importance of well-designed monitoring programs for the conservation of endangered species: case study of the snail kite. Conservation Biology 21, 472-481.

Martin, T., Wintle, B., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., A. Tyre, A. J., H. Possingham, H. P. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters 8, 1235-1246.

McCarthy, M. A., Moore, J. L., Morris, W. K., Parris, K. M., Garrard, G. E., Vesk, P. A., Rumpff, L., Giljohann, K. M., Camac, J. S., Bau, S. S., Friend, T., Harrison, B., Yue, B. 2013. The influence of abundance on detectability. Oikos 122, 717-726.

Moore, J. E., Swihart, R. K. 2005. Modeling patch occupancy by forest rodents: incorporating detectability and spatial autocorrelation with hierarchically structured data. The Journal of Wildlife Management 69, 933-949.

Newton, I., 2006. Advances in the study of irruptive migration. Ardea 94, 433-460

Post van den Burg, M., Bly, B., VerCauteren, T., Tyre, A. 2011. Making better sense of monitoring data from low density species using a spatially explicit modeling approach. Journal of Applied Ecology 48, 47-55.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rangel, T. F., Diniz-Filho, J. A. F., Bini, L. M. 2010. SAM: a comprehensive application for Spatial Analysis in Macroecology. Ecography **33**, 46-50.

Reynolds, J. H., Thompson, W. L., Russell, B. 2011. Planning for success: Identifying effective and efficient survey designs for monitoring. Biological Conservation 144, 1278-1284.

Rhodes, J. R., Jonzén, N. 2011. Monitoring temporal trends in spatially structured populations: how should sampling effort be allocated between space and time? Ecography 34, 1040-1048.

Rota, C. T., Fletcher Jr, R. J., Dorazio, R. M., Betts, M. G. 2009. Occupancy estimation and the closure assumption. Journal of Applied Ecology 46, 1173-1181.

Royle, J. 2006. Site occupancy models with heterogeneous detection probabilities. Biometrics 62, 97-102.

Royle, J. A., Kéry, M., Gautier, R., Schmid, H. 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. Ecological Monographs 77, 465-481.

Royle, J. A., Nichols, J. D. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84, 777-790.

Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J., van Bommel, F. P. J. 2006. Long-term population declines in Afro-Palearctic migrant birds. Biological Conservation 131, 93-105.

Sargeant, G., Solvada, M., Slivinski, C., Johnson, D. 2005. Markov chain Monte Carlo estimation of species distributions: a case study of the swift fox in western Kansas. Journal of Wildlife Management 69, 483-497.

Stojanovic, D., Webb, M. H., Alderman, R., Porfirio, Heinsohn, R. In press. Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird. Diversity and Distributions.

Tiefelsdorf, M. 2000. Modeling spatial processes: the identification and analysis of spatial relationships in regression residuals by means of Morans' I. Cambridge University Press, Cambridge.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., K. Parris, and H. P. Possingham.

2003. Improving precision and reducing bias in biological surveys: estimating false negative error rates. Ecological Applications 13, 1790-1801.

Webb, M. H., Holdsworth, M. C., Webb J. 2012. Nesting requirements of the endangered Swift Parrot (*Lathamus discolor*). Emu 112, 181-188.

Welsh, A. H., Lindenmayer, D. B., Donnelly, C. F. 2013. Fitting and interpreting occupancy models. PLoS ONE 8:e52015.

Wintle, B. A., Bardos, D. C. 2006. Modeling species-habitat relationships with spatially autocorrelated observation data. Ecological Applications 16, 1945-1958.

Wintle, B. A., McCarthy, M. A., Parris, K. M., Burgman, M. A. 2004. Precision and bias of methods for estimating point survey detection probabilities. Ecological Applications 14, 703-712.

Wintle, B. A., Runge, M. C., Bekessy, S. A. 2010. Allocating monitoring effort in the face of unknown unknowns. Ecology Letters 13, 1325-1337.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. Journal of the American Statistical Association 99, 673-686.

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H., Veran, S. 2013. Presence-only modelling using MAXENT: when can we trust the inferences? Methods in Ecology and Evolution 4, 236-243.

Yee, T. 2010. The VGAM package for categorical data analysis. Journal of Statistical Software 32, 1-34.

CHAPTER 4: The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems

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ABSTRACT

The distribution of mobile species in dynamic systems can vary greatly over time and space. Estimating their population size and geographic range can be problematic, with serious implications for conservation assessments. Scarce data on mobile species and the resources they need can also limit the type of analytical approaches available to derive such estimates. Here we quantify dynamic change in availability and use of key ecological resources required for breeding (i.e. food and nesting sites) for a critically endangered nomadic habitat specialist, the swift parrot (*Lathamus discolor*). We compare estimates of occupied habitat (km^2) derived from dynamic presence-background data climatic models to those derived from dynamic occupancy models that include a direct measure of food availability. We also compare estimates that incorporate fine resolution information on key ecological resources (i.e functional habitats) into distribution maps with more common approaches that typically focus on broader climatic suitability. For all models, both the extent and spatial location of occupied areas varied dramatically over the study period. The occupancy models produced significantly smaller (up to an order of magnitude) and more spatially discrete estimates of occupied habitat than climate-based models. Estimates accounting for the area of functional

habitats were also significantly smaller than estimates based only on occupied habitat. Importantly, an increase (or decrease) in one functional habitat did not necessarily correspond to changes in the other, with consequences for overall habitat functionality. We argue that these patterns are typical for mobile resource specialists, but currently go unnoticed due to limited data on (1) species' presence/absence and (2) availability of key resources. Understanding changes in the relative availability of functional habitats is crucial to informing conservation planning and accurately assessing extinction risk for mobile resource specialists.

INTRODUCTION

Predicting the distribution of nomadic migrants that respond to dynamic pulses in resource availability by exploiting rich patches is a major challenge for conservation planning (Woinarski et al. 1992). These species vary markedly in life history strategies, movement patterns and settlement cues (Dean 2004; Newton 2006), and their settlement patterns are poorly understood. In addition, they are often resource specialists, which can make them vulnerable to resource bottlenecks in time and space (Runge et al. 2014). Conservation of nomadic migrants depends on understanding where and when resources are available and how populations respond to resource configuration, (Runge et al. 2015a). Ecologically relevant and spatiotemporally explicit estimates of these species distributions are needed to guide conservation planning (Gaston & Fuller 2009) and accurately assess exposure to threatening processes (Runge et al. 2015b).

Species distribution models (SDMs) are increasingly used to guide conservation planning by characterizing a species' ecological requirements and projecting this over unsampled areas

(Guisan & Zimmerman 2000). The relative benefits of different modeling approaches have received considerable attention (Hastie & Fithian 2013; Guillera-Arroita et al. 2015). Models derived from systematically collected data on species' presences and absences perform better in terms of avoiding false positive and false negative errors than those based on less robust sampling designs (Guillera-Arroita et al. 2015). However, few nomadic migrants in dynamic environments have been studied using systematic sampling designs at ecologically relevant, large spatial scales, partly due to logistic or funding constraints. Hence limited data availability, especially the lack of absence records, can limit modeling approaches to less accurate presence-background techniques (Phillips et al. 2006). Another common limitation when modeling species distributions is that the resolution of spatial data layers used to predict a species' distribution may not reflect the resolution of the species' habitat use. Most SDMs are derived from macro-scale environmental characteristics (e.g. temperature, rainfall, vegetation cover) (Gaston & Fuller 2009) because continuous fine scale data on specific resources (e.g. food) are rarely available and often impractical to collect. If fine-scale habitat features determine species occurrence (hereafter: functional habitats), a species' occupancy of the landscape is likely to be overestimated in SDMs that do not account for them (Gaston & Fuller 2009). For habitat specialists this effect is magnified because broad-scale environmental data rarely capture higher resolution heterogeneity of functional habitats (Jetz et al. 2008). Species also often require spatial and temporal co-occurrence of different resources (eg. food near nests - Brambilla & Saporetti 2014). Incorporating functional habitats into SDMs together with both presence and absence data is likely to improve model estimates and transferability of predictions to unsampled areas, but published examples are rare (eg. Vanreusel et al. 2007; Araújo & Luoto 2007).

Despite these challenges, there is increasing demand for accurate and fine-scale distribution maps to guide conservation planning for threatened species. We explore factors affecting accurate distribution modeling for a critically endangered nomadic migrant, the swift parrot (*Lathamus discolor*) (Heinsohn et al. 2015). Settlement patterns of swift parrots are determined by local pulses of food availability over a large potential range (Webb et al. 2014). This dynamic and unpredictable system has proven a major challenge for implementing effective conservation action (Allchin et al. 2013) that accounts for spatial variation in the location and availability of breeding habitat, as well as likely changes in the relative availability of functional habitats. Deforestation of swift parrot breeding habitat continues (Supporting Information) without a clear understanding of the implications of the loss of particular sites and the effect on local habitat quality. Information about the spatial ecology of swift parrots is fundamental to their conservation because managing anthropogenic and predator impacts (Stojanovic et al. 2014; Heinsohn et al. 2015) on their population is dependent on understanding how swift parrots move through their large range. In this context, the implications of using different modeling approaches to estimate dynamic distributional changes in occupied functional habitats is crucial to conservation planning (Jetz et al. 2008).

We use data from a unique multi-year swift parrot monitoring program to quantify change in the use and availability of functional habitats over the breeding range. Using data sampled from each functional habitat, our aims were to: (1) compare estimates of occupied habitat derived from presence-background modeling incorporating climatic predictors, with estimates from occupancy modeling incorporating absence data and a direct measure of food, (2) quantify changes in the relative availability of different functional habitats over time, and (3) determine if variation in occupancy rates in one functional habitat is associated with

changes in the other. We discuss our results in the context of knowledge gaps for mobile species that exploit rich patches of food in dynamic systems, and the potential shortcomings for conservation planning when data on functional habitats are limited.

METHODS

Study system and species

Swift parrots are nectarivorous, tree cavity nesting nomadic migrants that move between their wintering range on mainland Australia to the island of Tasmania to breed during the austral summer (Higgins 1999). Breeding swift parrots need the flower of eucalyptus trees for food (Webb et al. 2014) and tree cavities for nesting (Webb et al. 2012). Variable but spatially structured flowering events of blue (*Eucalyptus globulus*) and black gum (*E. ovata*), determine settlement patterns of nesting swift parrots (Webb et al. 2014), meaning that the nesting locations change annually, and can be separated by up to hundreds of kilometers.

Standardized surveys in potential foraging habitat were carried out for swift parrots over their entire core breeding range (Natural Values Atlas 2015) between 2009 and 2014. Survey methods are outlined by Webb et al. (2014), but briefly, several hundred sites (range: 771-1034) were surveyed in eastern Tasmania (~10, 000 km^2) during October each year (i.e. the early breeding season) to collect detection/non-detection data using repeated five-minute counts. Survey sites were located in potential foraging habitat (i.e. ≥1 food tree within 200 m of the site centroid). Food trees were surveyed for flowering and scored on a scale of 0 to 4, where 0= no flower, 1= light, 2= moderate, 3= heavy and 4= very heavy.

Comparing distribution estimates using presence-background vs. presence-absence approaches

(i) Habitat suitability models

To derive the distribution of swift parrots using a standard presence-background data approach we fitted annual models of habitat suitability using Maxent v3.3.3 (Phillips et al. 2006). We built annual time-sliced distribution maps for the period November 2009 to November 2012, matching species occurrence data with site-specific environmental conditions over the preceding 12 months before each observation. Daily weather data were unavailable for 2013 and 2014, and these years could therefore not be included in this component of the analysis. This resulted in four annual distribution maps (see Runge et al., 2015b for further details of the modeling approach). A 12-month time lag was chosen because this lag had the strongest predictive power (3, 6, 9, and 12-month lags were compared using the Area Under the Curve, AUC). We used annual time-sliced models because we suspect the use of an area in one year was independent of habitat use in previous years (i.e. no site fidelity), a characteristic of many mobile species that rely on fluctuating resources.

The annual distribution maps were created by first populating fine-resolution monthly rasters with six different weather variables for each 100m x 100m grid cell in Tasmania over the preceding 12 months: total rainfall (mm), average rainfall, maximum temperature (^{o} Celsius), minimum temperature, average maximum daily temperature, average minimum daily temperature (Xu & Hutchinson 2011). A spatial layer of eucalypt forest was also converted to a 100m x 100m resolution raster to represent potential habitat (TASVEG 3.0; DPIPWE 2013). All variables were checked for correlations - other weather variables were considered but were correlated with at least one of the above variables. Next, a global model of swift

parrot responses to environmental conditions based on all swift parrot occurrences from 2009 to 2012 (n=477) was created using Maxent, with 10% of records reserved for model validation. This global model was then projected across the environmental conditions in the study region during the 12 months preceding November each year (approximate midpoint of the swift parrot nesting season).

We reclassified the Maxent logistic output into predictions of presence or absence using equal sensitivity and specificity threshold values for each year (Liu et al. 2013). This resulted in a map of predicted presence or absence for each year from 2009 to 2012.

(ii) Occupancy models representing functional requirements

To estimate species distribution based on detection/non-detection data and food availability we used occupancy models published by Webb et al. (2014), updating them to include two additional years of data (resulting in a time series from 2009-2014). Using data from each year we modelled annual occupancy probabilities (Ψ) and incorporated imperfect detection (p) in zero-inflated binomial models (ZIB) using the EM Algorithm to allow the inclusion of a Generalized Additive Model (GAM) in the occupancy component of the ZIB (Webb et al. 2014). Flower score and a bivariate smoothed spatial term (latitude, longitude) were used as covariates in the Ψ component, with flower score as the single covariate in the p component. Model predictions were interpolated across the study area using kriging at 0.02^{o} resolution (~1.6x1.6 km) with a neighborhood search radius of 0.05^{o} (~5 km) (sensu Webb et al. 2014). We considered these scales to be ecologically relevant based on the degree of spatial autocorrelation in each year (Webb et al. 2014). Again, we assumed the species' distribution in each year to be resource driven and therefore independent of other years.

To produce a binary map of swift parrot occurrence we reclassified Ψ into predictions of presence or absence using a minimum threshold value for each annual model that represented the mid-point between average Ψ values for occupied and unoccupied sites from our monitoring data (Fielding & Haworth 1995).

Estimating temporal change in occupied habitat

Using species distribution outputs from the habitat suitability and occupancy models, we derived annual estimates of occupied habitat based on two scenarios that reflected different underlying assumptions about habitat availability : (1) TOTAL AREA (area of all cells identified as suitable or occupied), and (2) FOREST (area of all eucalypt forest and woodland in cells identified as suitable or occupied). Areas falling outside the swift parrot breeding range (Natural Values Atlas 2015) were excluded from estimates.

To better account for swift parrot habitat specialization we estimated occupied habitat within the species' two key functional habitats: (1) foraging habitat containing blue or black gums, and (2) nesting habitat containing mature, cavity bearing trees (i.e. functional habitat area). For these analyses we used two different spatial layers that identified each functional habitat. For foraging habitat, we used a spatial polygon layer categorizing the contribution of blue or black gum to forest canopy cover (DPIPWE 2010). For nesting habitat, we used a spatial polygon layer of mature forest that reflects a higher probability of the presence of tree cavities (Forest Practices Authority 2011). To reduce uncertainty, we excluded foraging habitat polygons with <5% blue or black gum and those where tree diameter at breast height was <40 cm (flowering of young trees is weak and rarely provides an attractive resource - Brereton et al. 2004). Polygons of the mature forest layer were included in the analysis if they

were categorized as low (5-20%), medium (20-40%) or high (>40%) density of mature tree crowns (Stone 1998). The mature forest cover layer was updated using the 30 x 30 m remotely-sensed Global Forest Change Layer (Hansen et al. 2013) to account for recent deforestation (also see Supporting Information).

Three estimates of functional habitat area were derived from both the habitat suitability models and the occupancy models. Firstly, we intersected the final output of each model in each year with the foraging habitat layer or the mature forest layer to derive estimates of (i) FORAGING HABITAT and (ii) NESTING HABITAT respectively. Then, we derived another estimate of nesting habitat, (iii) ADJUSTED NESTING HABITAT, to account for variation in the density of mature trees, and thus the likely density of tree cavities. To do this we first reclassified the crown cover category for each polygon of the mature forest layer by dividing the area of each polygon by the median value of its crown cover category (12.5%, 30% and 60% respectively). Total functional habitat area was then calculated by summing FORAGING HABITAT and ADJUSTED NESTING HABITAT.

We compared different estimates of occupied habitat derived from habitat suitability maps versus occupancy maps using Pearson's product-moment correlations. To determine whether these estimates followed the same trends over time when derived from different models, we used analysis of covariance (ANCOVA) to compare trends in the slopes of regressions of the estimates from different modeling approaches.

Estimating occupancy rates in nesting habitat

To validate our models and estimate 'true' occupancy rates in nesting habitat, we also surveyed potential nesting habitat of swift parrots annually during November-December between 2009 and 2014 (i.e. after the survey of foraging habitat described above and timed to coincide with the mid nesting period). Sampling locations were established in the nearest potential nesting habitat (i.e. mature forest) to foraging sites where swift parrots were detected. After marking an initial sampling location, the observer moved >200 m away on a random compass bearing to mark the next site. Sampling locations had at least one potential nest tree using the descriptions outlined in Webb et al. (2012). Swift parrot detection/non-detection data were recorded within a 100 m radius around each sampling location. Provisioning swift parrots forage mostly within a 5 km radius of their nests (D. Stojanovic, unpublished data) so we included nesting survey sites if they were within 5 km of the boundary of each occupancy model (with the threshold applied).

For each year we estimated swift parrot nesting occupancy (Ψ_n) and detectability (p_n) (MacKenzie et al. 2002) in nesting habitat captured by the respective threshold occupancy model using program PRESENCE (Hines 2012). We achieved spatial replication (with replacement) by placing a 1 km^2 grid over sampled areas, and each sampling location was treated as a repeat visit to each grid cell. The mean number of 1 km^2 cells sampled each year was 128 (SD 45), and the mean number of sampling locations per cell was 3.6 (SD 2.4) (Supporting Information). The number of sampling locations per cell was primarily influenced by the occurrence of potential nesting trees and access. Importantly, estimates of Ψ_n are conditional on the presence of potential nest trees because no surveys were conducted where likely nest trees were absent.

RESULTS

Presence-background vs. presence-absence approaches to mapping distribution

Habitat suitability models produced substantially different distribution maps to the occupancy models in terms of the locations predicted to be suitable or occupied over time (Fig. 1 and 2). Distribution maps based on habitat suitability models also captured significantly larger areas of the landscape compared with those based on occupancy models (i.e. 2 – 12 times larger depending on the measure of habitat used) (Table 1, Fig. 3). There was no significant correlation between habitat extent estimates based on the two different modeling approaches (Pearson's product-moment correlation; $p>0.05$, Supporting Information). Model summaries and the location of swift parrot detections are provided in Supporting Information.

Habitat suitability models captured 16 to 30% more occupied sites than the occupancy models in the four years climate data were available (Supporting Information), but they also predicted large areas (2618 – 4827 km^2) to be suitable in locations where the occupancy models provided strong evidence that swift parrots were either absent or present in only very low numbers. Mean occupancy probability outside areas captured by the occupancy models from 2009-2012 was 0.109 (SD 0.099) (Supporting Information). Occupancy models had a high degree of overlap with the habitat suitability models (mean: 78%, SD 8.7%, Supporting Information) but identified more spatially discrete regions of occupied habitat that reflected patterns of flowering in each year (Fig. 2).

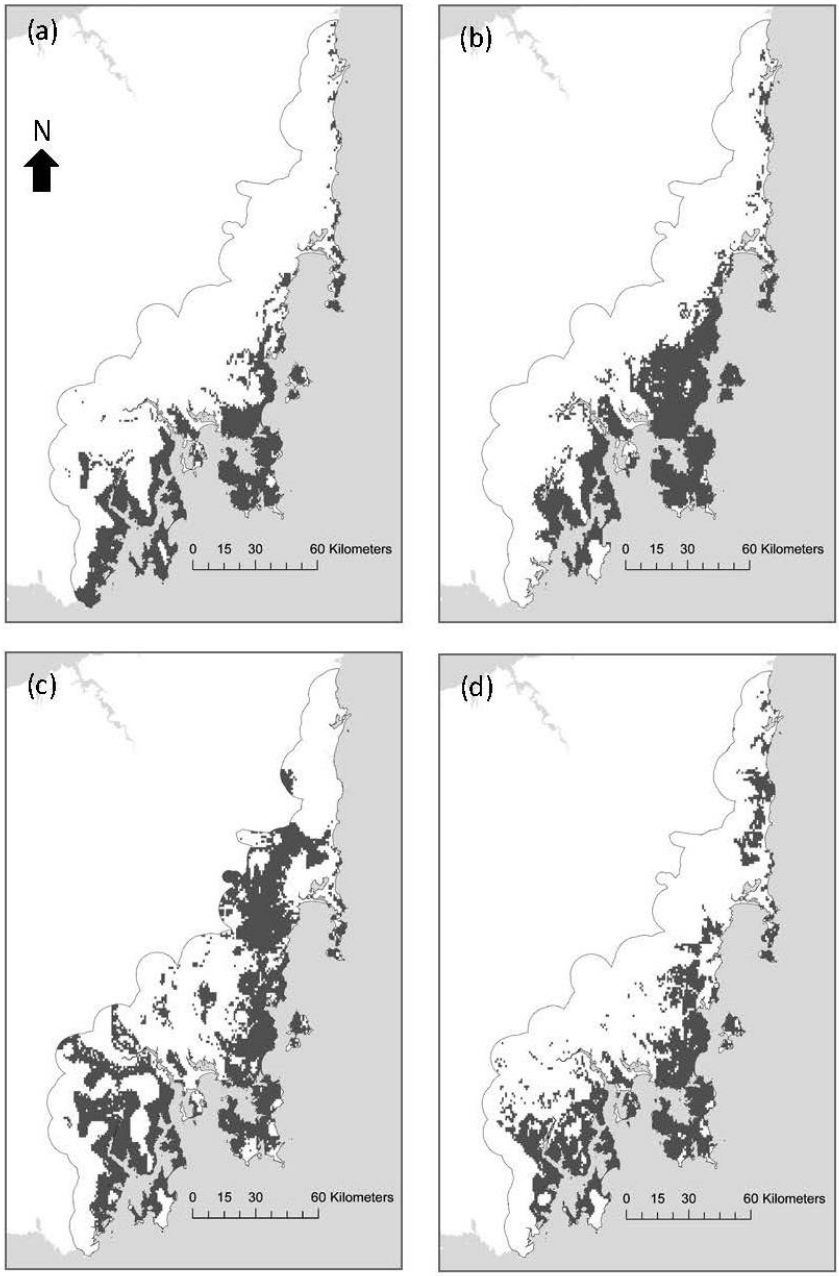

Figure 1. Habitat suitability models (using Maxent) from 2009-2012 (left to right a, b, c and d) using equal sensitivity and specificity threshold. Threshold values for each year were 0.1557, 0.2070, 0.2481, 0.1670, respectively. Grey line is the swift parrot breeding range (Natural Values Atlas 2015).

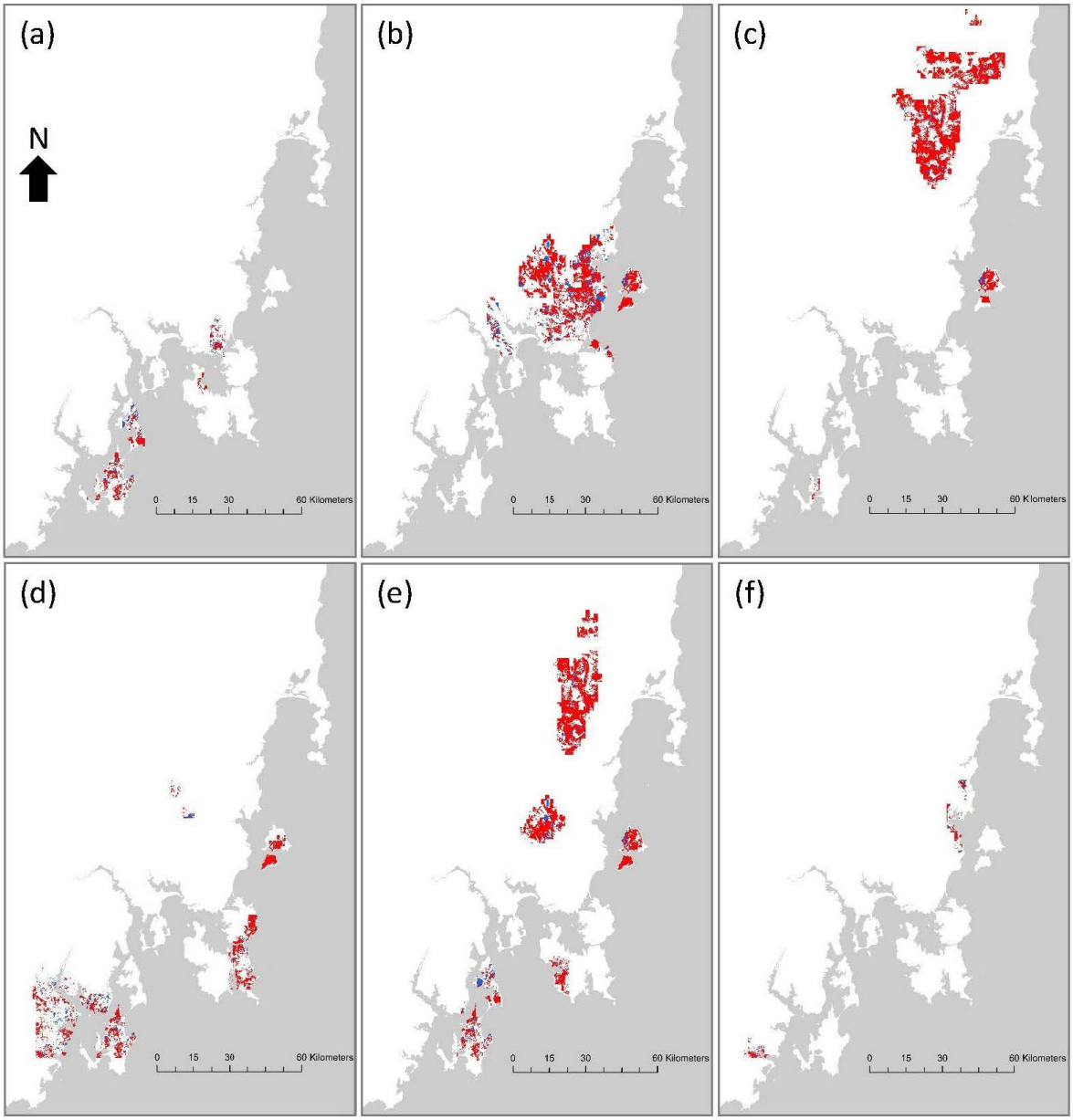

Figure 2. Swift parrot occupancy models from 2009-2014 (left to right a, b, c, d, e, f). NESTING HABITAT (red), FORAGING HABITAT (blue). Threshold values for each year were 0.3637, 0.3904, 0.4305, 0.3932, 0.3635, 0.2926, respectively.

Table 1. ANCOVA results testing for the effect of modeling approach and year on estimates of occupied habitat (model = habitat suitability model versus occupancy model).

Measure of habitat	Variable	*F*-value	*p*-value
TOTAL AREA	model	46.5	0.006
	year	1.2	0.48
FOREST	model	36.4	0.009
	year	2.0	0.31
NESTING	model	36.1	0.009
	year	2.1	0.29
ADJUSTED NESTING HABITAT	model	29.9	0.012
	year	2.3	0.26
FORAGING HABITAT	model	74.1	0.003
	year	1.1	0.51

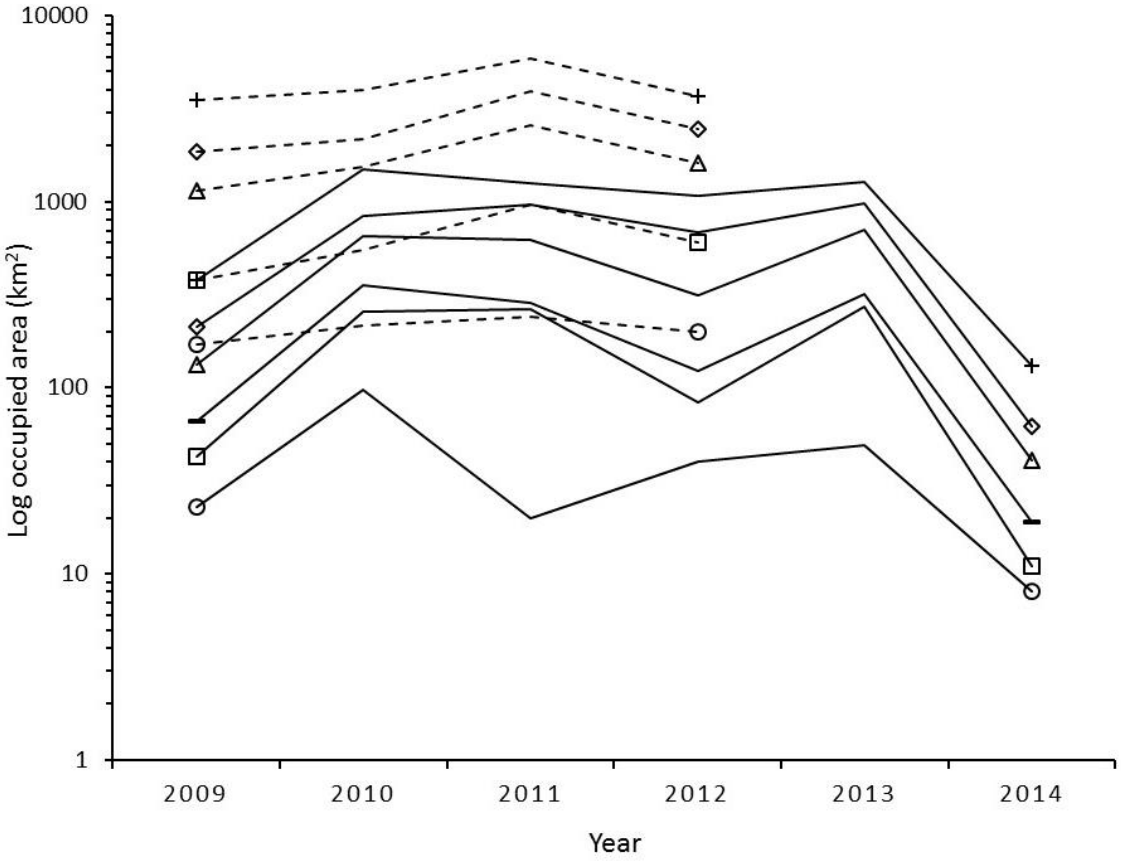

Figure 3. Annual estimates of occupied habitat from habitat suitability models (dashed lines) and occupancy models (solid lines) in the swift parrot breeding range over 6 years: + TOTAL AREA, ◊ FOREST, Δ NESTING HABITAT, □ ADJUSTED NESTING HABITAT, ○ FORAGING HABITAT, − Total functional habitat area; *Y* axis is on the logarithmic scale.

Temporal change in occupied habitat

There were large differences in the location of occupied habitat estimated using the occupancy models in each year (Fig. 2). Habitat extent derived from the occupancy models also varied dramatically between some years, particularly for functional habitats (up to three orders of magnitude, Fig. 3; see Supporting Information for individual estimates), although there was no significant trend over time (Table 1, $p>0.05$). Compared to the occupancy models, annual estimates of habitat extent derived from habitat suitability models varied less (Fig. 1, Table S5). Estimates of functional habitat areas were consistently and substantially smaller than other estimates using both modeling approaches, often by several orders of magnitude (Fig. 3). For the occupancy models, an increase or decrease in TOTAL AREA or FOREST did not correspond to a significant respective increase or decrease in FORAGING HABITAT ($p>0.05$, Table S2). Furthermore, an increase or decrease in availability of one functional habitat did not necessarily correspond to a significant increase or decrease in the other ($p>0.05$, Table S2, Fig. 3). Poor flowering conditions in 2014 resulted in only small isolated patches of foraging habitat being available and a dramatic reduction in all estimates of occupied habitat (Fig. 2 & 3). Notably, at a handful of sites (<10) captured by the 2014 occupancy model, unusually high abundances of swift parrots (estimated >300 individuals) appeared to be constantly present while local flowering persisted.

Occupancy rates in nesting habitat

Predicted swift parrot occupancy Ψ_n in nesting habitat was high in all years (0.69 to 0.94) except 2014, with a relatively constant detection rate of 0.49 (SD 0.09, Table 2). Interestingly, large annual variations in estimates of NESTING HABITAT and ADJUSTED NESTING HABITAT (Fig. 3) were not reflected in the respective annual changes in Ψ_n (Pearson's r = -0.33, p = 0.58; Pearson's r = -0.45, p = 0.45, respectively). Although the very

restricted functional habitat areas identified by the 2014 occupancy model were associated with very high densities of birds in a small area of foraging habitat (see above) this did not translate into high Ψ_n (or p_n) in nearby nesting habitat.

Table 2. Nesting occupancy (Ψ_n) and detectability (p_n) rates in surveyed nesting habitat.

	Year					
Parameter	2009	2010	2011	2012	2013	2014
Naïve Ψ_n	0.66	0.66	0.51	0.59	0.65	0.29
Ψ_n	0.74	0.83	0.69	0.94	0.74	*
SE	0.07	0.05	0.06	0.07	0.05	*
p_n	0.4	0.57	0.55	0.49	0.57	0.35
SE	0.03	0.03	0.04	0.03	0.03	0.04

Naïve Ψ_n = observed occupancy

* could not be estimated due to poor model fit

DISCUSSION

By linking estimates of geographic range size to changing availability of functional habitats for a nomadic migrant we provide a means to better understand the consequences of dynamic variation in species geographic distributions. Our estimates of functional habitat area from dynamic occupancy models provide a method for identifying where and when resource bottlenecks may occur. For example, although swift parrot breeding had previously been recorded at several locations identified in this study, we reveal that in some years most of the population is forced to rely on small areas of habitat. Our approach provides a sound basis for targeting conservation resources and allows spatially explicit thresholds to be set for functional habitats in the context of ongoing habitat loss and dynamic pulses in resource availability that can result in very small areas of suitable breeding habitat. Our study also demonstrates that assessment of spatiotemporal variation in exposure to other threats (eg. nest predation) may be improved with modeling approaches that account for ecologically relevant information (i.e. presence/absence of target species and functional habitats).

By modeling change in species occupancy and selecting only the functional habitat from annual distributions, we detected dynamic variation in ecologically relevant habitats that was not detected by more commonly applied habitat suitability models (Fig. 3). Significant differences between estimates of occupied habitat were dependent on the type and function of habitat considered and the modeling technique, and illustrated how the method utilized to calculate geographic range size can in itself cause non-trivial variation and uncertainty in occupancy estimates of potential habitat (Jiménez-Valverde et al. 2008). This may have important implications for assessing extinction risk of nomadic migrants because scarce data often limit modeling approaches that can be utilized for achieving conservation planning and

assessment objectives (Jetz et al. 2008; Runge et al. 2015b; Tulloch et al. 2016). In particular, the high rate of Type I errors (i.e. false positives) inherent in our habitat suitability models limits their application to conservation planning in a landscape with multiple competing land uses (e.g. industrial scale logging), and detecting trends over time. There will always be tradeoffs between the rate of Type I and Type II errors (Field et al. 2007); however, our occupancy models provide strong evidence on which to base conservation planning in an environment where habitat protection often has considerable economic implications for competing interests. Furthermore, our results demonstrate the importance of incorporating direct measures of resource availability into species distribution predictions, as well as distinguishing functional habitats in the environmental matrix.

Readily available presence-only data may be sufficient to understand the distributions of well-studied species, providing occurrence records cover important environmental gradients (Lentini & Wintle 2015). However, we show this may not be the case for specialized species with dynamic distributions. Our presence-background models used occurrence data collected in a spatially stratified, systematic sampling design, but yielded much larger estimates of swift parrot distribution over time compared to occupancy models. Sensitivity analyses revealed that these differences remained even when the threshold assigning species' presence/absence to the occupancy model results was reduced by 50% (Supporting Material). The strong over-prediction (i.e. higher Type I error rate) of the presence-background models is because they do not explicitly account for food availability or spatial location, and hence spatial structuring of the population each year (Estrada et al. 2016). Because flowering is also typically spatially structured (Webb et al. 2014), and is likely influenced by climatic variability, explicitly modeling flowering patterns (Giles et al. 2016) rather than birds may be

an interesting area of future research to predict changes in food availability and the occurrence of swift parrots (Woinarski et al. 2000).

We suggest the greater percentage of occupied sites captured by these models is a reflection of the species realized niche (while breeding) being greater than its fundamental niche (Pulliam 2000), likely resulting from limitation of one or both functional habitats. Alternatively, this may also be attributable to records of swift parrots that had not yet settled to breed. Unfortunately, most data for species with similarly variable distributions consist of presence-only records that have not been collected in a structured sampling design (Runge et al. 2015b). Our study highlights the value of investing in the acquisition of high quality (i.e. repeated, standardized) presence data *and* absence data for threatened nomadic migrants.

The small estimates of functional habitat area represent a sobering reality for a species experiencing widespread anthropogenic landscape change (Supporting Information) and spatially heterogeneous threats like nest predation. While the spatial location and extent of functional habitat areas varied considerably between years (Fig. 3), nesting occupancy remained consistently high until 2013 (up to 94%). This suggests either the abundance-occupancy relationship in nesting habitat varied between years, or some birds did not breed due to nesting site limitation, particularly in 2014 (Table 2). Moreover, even our detailed estimates of functional habitat area are likely to overestimate occupied habitat (e.g. Stojanovic et al. 2012, 2014b). Accurately quantifying resources at such fine resolutions is often not possible but important to consider, irrespective of the sophistication of modeling approaches (Collier et al. 2012).

The relative availability and spatial configuration of functional habitats for mobile species has important ramifications for the fitness of individuals and carrying capacity within occupied areas (Brambilla & Saporretti 2014; Olsson & Bolen 2014). The fitness of swift parrots is improved by breeding in the richest patch of food available in the landscape (Stojanovic et al. 2015) but nest site availability will determine how many birds will be able to breed in a given patch. For example, as swift parrot settlement patterns changed over time, an increase/decrease in one functional habitat did not necessarily correspond to an increase/decrease in the other (Fig. 3). For species that experience dynamic change in geographic distribution, an increase in the extent of occupied area may not equate to better habitat quality or function. Rather, habitat quality is contingent on the relative availability and overlap of key functional habitats. Our study indicates that the temporal availability of one functional habitat (e.g. nesting sites) can be restricted due to the absence of another key resource (e.g. foraging resources). When the availability of one or both functional habitats for the swift parrot falls below an (as yet undefined) threshold it may restrict settlement options and limit breeding participation. We argue that many nomadic migrants experience resource bottlenecks due to limitation of one or more functional habitats, but these bottlenecks go unmeasured due to data deficiency and lack of rigorous research (Newton 2012).

By incorporating a direct measure of food availability and high resolution mapping of functional habitat features, we derived ecologically relevant and mechanistically-informed estimates of occupied swift parrot breeding habitat. Even when a species appears to occupy a large area, resource dependence may mean only a small fraction of that area can actually be exploited (eg. Jetz et al. 2008). Hence, the loss of small areas of one (or both) functional habitats can have profound effects on the population and negate potential benefits from conservation actions elsewhere (Runge et al. 2015a). Given the spatial and temporal scale at

which habitat loss and disturbance are occurring in the swift parrot breeding range (Supporting Information), we argue that spatially discrete regions should be managed in a way that reflects the availability of functional habitats at ecologically relevant scales and their importance to the population in a given year. For example, the foraging range of swift parrots from a nest site is one relevant scale to consider. Similarly, the scale (and location) at which breeding aggregations occur, such as those identified in this study, are important at the population-level. The availability of functional habitats at these two scales, in combination with changing flowering conditions, determines the carrying capacity of the breeding range in a given year, particularly during resource bottlenecks. Therefore, habitat management that does not consider the spatial location, scale and relative availability of specific habitats is likely to be less effective.

Nomadic migrants are a chronically understudied species guild, but represent an important component of animal movement strategies (Dingle 1996). Many nomadic species require urgent conservation attention (Faaborg et al. 2010) but a lack of robust data can be a serious impediment to conservation assessment and effective conservation actions. We encourage conservation agencies to recognize the limitations of using distribution models derived from incomplete data (see also Tulloch et al. 2016), and to develop conservation plans that account for functional habitats where possible. Integrating temporal change in resource availability into conservation planning for mobile species is challenging but critical to identifying key locations, dependencies among habitats and sites, and exposure to other threats (Runge et al. 2016). To address this challenge, investing in the collection of both high quality occupancy and environmental data to estimate species distributions should be a priority. In the absence of such information, many knowledge gaps for nomads will continue to go unaddressed, leading to inaction or poorly directed resources that provide little conservation benefit.

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SUPPORTING INFORMATION

Map of forest loss/disturbance between ~1997-2013 (Appendix S1); Occupancy models showing sites where swift parrots were observed in each of the six years (Appendix S2); occupancy model and Maxent model summaries; information on number of sampling locations for surveys in nesting habitat; comparison of estimates from different modeling approaches; percentage of occupied sites captured by habitat suitability and occupancy models; mean occupancy probabilities outside areas captured by occupancy models; annual estimates of occupied habitat from each modeling approach (Appendix S3); sensitivity analysis examining the effect of reducing the threshold assigning species' presence/absence to the occupancy models (Appendix S4).

REFERENCES

Allchin R, Kirkpatrick J, Kriwoken L. 2013. On not protecting the parrot: Impact of conservation and planning legislation on an endangered species in Tasmania. Journal of Wildlife Law and Policy **16:**81-104.

Araújo MB, Luoto M. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography **16:**743-753.

Brambilla M, Saporetti F. 2014. Modelling distribution of habitats required for different uses by the same species: Implications for conservation at the regional scale. Biological Conservation **174:**39-46.

Brereton R, Mallick SA, Kennedy SJ. 2004. Foraging preferences of Swift Parrot on Tasmanian Blue-gum: tree size, flowering frequency and flowering intensity. Emu **104:**377-383.

Collier BA, Groce JE, Morrison ML, Newnam JC, Campomizzi AJ, Farrell SL, Mathewson HA, Snelgrove RT, Carroll RJ, Wilkins RN. 2012. Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. Diversity and Distributions, **18:**158-167.

Dean WRJ. 2004 Nomadic desert birds. Springer-Verlag, Berlin, Heidelberg.

Department of Primary Industries Parks, Water and Environment (DPIPWE). 2010. GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

Department of Primary Industries, Parks, Water and Environment (DPIPWE). 2013. TASVEG 3.0. Tasmanian Vegetation Monitoring and Mapping Program, Tasmanian Government, Hobart.

Dingle H. 1996. Migration. The Biology of Life on the Move. Oxford University Press Inc., New York.

Estrada A, Delgado MP, Arroyo B, Traba J, Morales MB. 2016. Forecasting large-scale habitat suitability of European Bustards under climate change: The role of environmental and geographic variables. PLOS ONE **11:** (e0149810) DOI: 10.1371/journal.pone.0149810

Faaborg J, et al. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications **20**:398-418.

Field SA, O'Conner PJ, Tyre AJ, Possingham HP. 2007. Making monitoring meaningful. Austral Ecology **32:**485-491

Fielding A, Haworth, PF. 1995. Testing the generality of bird-habitat models. Conservation Biology **9:**1466–1481.

Forest Practices Authority. 2011. Potential hollow availability map, Fauna Technical Note No. 2. Forest Practices Authority, Hobart.

Gaston KJ, Fuller, RA. 2009. The sizes of species' geographic ranges. Journal of Applied Ecology **46:**1-9.

Giles JR, Plowright RK, Eby P, Peel AJ, McCallum H. 2016. Models of Eucalypt phenology predict bat population flux. Ecology and Evolution **6:**7230-7245

Guillera-Arroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kajula, H, Lentini PE, McCarthy MA, Tingley R, Wintle BA. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography **24:**276-292.

Guisan A, Zimmerman N. 2000. Predictive habitat distribution models in ecology. Ecological Modelling **135:**147-186.

Hansen MC, et al. 2013. High-Resolution Global Maps of 21st Century Forest Cover Change. Science **342:**850-853.

Hastie T, Fithian W. 2013. Inference from presence-only data; the ongoing controversy. Ecography **36:**864-867.

Heinsohn R, Webb M, Lacy R, Terauds A, Alderman R, Stojanovic D. 2015. A severe predator-induced population decline predicted for endangered, migratory swift parrots (*Lathamus discolor*). Biological Conservation **186:**75-82.

Higgins PJ. (Ed.), 1999. Handbook of Australian, New Zealand and Antarctic Birds, Volume 4, Parrots to dollarbird. Oxford University Press, Melbourne.

Hines JE. 2012. PRESENCE 10.4 – Software to estimate patch occupancy and related parameters. USGS-PWRC. Available from: http://www.mbr-pwrc.usgs.gov/software/presence.html

Jetz W, Sekercioglu CH, Watson JEM. 2008. Ecological correlates and conservation implications or overestimating species geographic range sizes. Conservation Biology **22:**110-119.

Jiménez-Valverde A, Lobo JM, Hortal J. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. Diversity and Distributions **14:**885-890.

Lentini PE, Wintle BA. 2015. Spatial conservation priorities are highly sensitive to choice of biodiversity surrogates and species distribution model type. Ecography **38:**1101-1111.

Liu C, White M, Newell G. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography **40:**778-789.

MacKenzie D, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83:**2248-2255.

Natural Values Atlas (www.naturalvaluesatlas.tas.gov.au). 2015. © State of Tasmania. (accessed 1 September 2015)

Newton I. 2006. Advances in the study of irruptive migration. Ardea **94:**433-460.

Newton I. 2012. Obligate and facultative migration in birds: ecological aspects. Journal of Ornithology **153**:S171-S180.

Olsson O, Bolen A. 2014. A model for habitat selection and species distribution derived from central place foraging theory. Oecologia **175:**537-548.

Phillips S, Anderson R, Schapire R. 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling **190:**231–259.

Pulliam HR. 2000. On relationship between niche and distribution. Ecology Letters **3:**349-361.

Runge C A, Martin TG, Possingham HP, Willis SG, Fuller RA. 2014. Conserving mobile species. Frontiers in Ecology and the Environment **12:**395-402.

Runge CA, Watson JEM, Butchart SHM, Hanson JO, Possingham HP, Fuller RA. 2015a. Protected areas and global conservation of migratory birds. Science **350:**1255-1258.

Runge CA, Tulloch A, Hammill E, Possingham HP, Fuller RA. 2015b. Geographic range size and extinction risk assessment in nomadic species. Conservation Biology **29:**865-876.

Runge CA, Tulloch AIT, Possingham HP, Tulloch V, Fuller RA. 2016. Incorporating dynamic distributions into spatial prioritization. Diversity & Distributions **22:**332-343.

Stojanovic D, Webb MH, Roshier D, Saunders D, Heinsohn R. 2012. Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered Swift Parrot. Emu **112:**350-356.

Stojanovic D, Webb M, Alderman R, Porfirio LL, Heinsohn R. 2014a. Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird. Diversity and Distributions **20:**1200-1207.

Stojanovic D, Koch AJ, Webb M, Cunningham R, Roshier D, Heinsohn R. 2014b. Validation of a landscape-scale planning tool for cavity-dependent wildlife. Austral Ecology **39:**579-586

Stojanovic D, Terauds A, Westgate MJ, Webb MH, Roshier DA, Heinsohn R. 2015. Exploiting the richest patch has a fitness payoff for the migratory swift parrot. Journal of Animal Ecology **84:**1194-1201.

Stone M. 1998. Forest-type mapping by photo interpretation: a multi-purpose base for Tasmania's forest management. Tasforests **10:**15–32.

Tulloch AIT, Sutcliffe P, Naujokaitis-Lewis I, Tingley R, Brotons L, Ferraz KMPMB, Possingham H, Guisan A, Rhodes JR. 2016. Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and

ecological processes. Biological Conservation, **199:**157-171.

Vanreusel W, Maes D, van Dyck H. 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. Conservation Biology **21:**201-212.

Webb MH, Holdsworth, MC, Webb J. 2012. Nesting requirements of the endangered Swift Parrot (*Lathamus discolor*). Emu **112:**181-188.

Webb MH, Wotherspoon S, Stojanovic D, Heinsohn R, Cunningham R, Bell P, Terauds A. 2014. Location matters: using spatially explicit occupancy models to predict the distribution of the highly mobile, endangered swift parrot. Biological Conservation **176:**99-108.

Woinarski JCZ, Whitehead PJ, Bowman DMJS, Russell-Smith J. 1992. Conservation of Mobile Species in a Variable Environment: The Problem of Reserve Design in the Northern Territory, Australia. Global Ecology and Biogeography Letters **2:**1-10.

Woinarski JCZ, Connors GC, Don F. 2000. Thinking honeyeater: nectar maps for the Northern Territory, Australia. Pacific Conservation Biology **6:**61-80.

Xu T, Hutchinson M. 2011. ANUCLIM version 6.1 user guide. The Australian National University, Fenner School of Environment and Society, Canberra.

CHAPTER 5: An empirical and mechanistic explanation of the abundance-occupancy relationship for a critically endangered nomadic migrant.

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ABSTRACT

A positive abundance-occupancy relationship (AOR) is a pervasive pattern in macroecology, implying that species occupying more sites are more locally abundant, but causality is often hard to determine. Conservation planning relies heavily on the assumption of a positive association between abundance and occupancy, usually assuming the relationship remains constant over short time frames. Examples of AORs being measured for highly mobile nomadic species with variable distributions are extremely rare, but they provide ideal opportunities for exploring these relationships. We examined temporal and spatial trends in the AOR over 7 years for a critically endangered nomadic migrant, the swift parrot, which relies on dynamic pulses in food availability and suitable tree cavities to breed. We predicted a negative temporal relationship where local mean abundances increase when the number of occupied sites decreases, and a positive but variable spatial relationship, whereby local abundances increase with the probability of occurrence. The temporal AOR was negative (p <0.01). Annual food availability was positively correlated with the number of occupied sites (p <0.01) and negatively correlated with abundance (p < 0.05). Thus, as food availability decreased, local densities of birds increased, and visa-versa. Generalised additive models showed the relationship between abundance and the probability of occupancy was positive and non-linear, but the nature of the relationship varied between years due to differing degrees of spatial aggregation caused by spatiotemporal changes in food availability. Importantly, high abundance (or occupancy) does not necessarily equate to high quality

habitat and may be indicative of resource bottlenecks or exposure to other processes affecting vital rates. Our results provide a rare empirical example that highlights the complexity of AORs for nomadic species with variable distributions and changing resource availability.

INTRODUCTION

A well-documented pattern in ecology, both within and among species, is that species occupying more sites or with larger geographic distributions are generally more locally abundant at sites they occupy, resulting in a positive abundance-occupancy relationship (Brown 1984; Gaston & Lawton 1990; Borregaard & Rahbek 2010). This implies that if the local abundance of a species is reduced (e.g. by degradation of habitat), then the number of sites that it occupies will also be reduced, even if the environmental or anthropogenic threatening processes are not occurring across all of the sites (Gaston and Curnutt 1998). Research into the abundance-occupancy relationship (AOR) has covered a wide range of taxa (e.g. Gaston et al.1998; Conrad et al. 2001; Kotze *et al*. 2003; Blackburn et al. 2006; Webb et al. 2007; Buckley et al. 2010; Verberk et al. 2010; Faulks et al. 2015), and has numerous implications for population monitoring and management (Gaston 1999), biological invasions (Kulhanek et al. 2011), pest management (Wilson & Room 1983) and setting harvest limits (Gaston et al. 2000; Buckley et al. 2017).

Nomadic migrants are at high global risk of extinction (Cottee-Jones et al. 2015) and conservation planning for them is in its infancy (Runge et al. 2014; Runge et al. 2015b). Despite this group of species representing a common movement strategy (Runge et al. 2015a) successful research on these them is rarely achieved at appropriate scales (Dingle 2008) resulting in a paucity of high quality data sets. Hence, few studies have examined trends in intraspecific AORs or predictions of spatial and temporal patterns in the probability of occupancy and abundance for nomadic migrants. However, developing a better empirical and

mechanistic understanding of these relationships for nomads may provide urgently needed guidance to inform conservation planning. Generally, nomads have highly variable range sizes over time, specialised requirements and the capacity to move long distances in response to changing resource availability (e.g. food) (Newton 2006). Because they often undergo short-term natural dynamic change in their distributions and density, nomads provide interesting opportunities for exploring the causal mechanisms driving AORs (Gaston et al. 1998; Freckleton et al. 2005; Webb et al. 2012). Here we provide a rare empirical explanation of spatiotemporal dynamics in the abundance-occupancy relationships for a critically endangered nomadic migrant, the swift parrot (*Lathamus discolor*). During breeding the species exploits dynamic and spatially structured pulses in tree flowering (for food) and requires the co-occurrence of tree cavities (for nesting). This results in the population shifting its breeding locations *en masse* from one year to the next (Webb et al. 2017).

Conservation planning often relies heavily on the assumption of a positive relationship between abundance and occupancy probabilities (e.g. Maclean et al. 2011; Collier et al. 2012; Heinsohn et al. 2015). This assumption allows species occupancy (or other suitability indices) at sites to be used as surrogates for abundance (Weber et al. 2016) and usually implies that there is a direct relationship between habitat quality and a species' abundance (e.g. Freckleton et al. 2005; Mosser et al. 2009). Temporal trends in AORs have received less attention (Webb et al. 2007) and most studies also assume the relationship remains constant over relatively short time frames (e.g. Maclean et al. 2011; Gutiérrez et al. 2013). We test the applicability of these assumptions for the nomadic swift parrot in its breeding range.

Several hypotheses and causal mechanisms have been proposed to explain the existence and nature of AORs. Broadly speaking, these hypotheses can be divided into three categories (*sensu* Faulks et al. 2015 and references therein): (1) niche breadth in relation to abiotic and/or biotic factors (Brown 1984; Holt et al. 1997; Freckleton et al. 2006;); (2) population

dynamics mediated by dispersal and colonisation (Freckleton et al. 2005); and (3) sampling artefacts resulting from range position and the sampling resolution (Gaston et al. 2000; He and Gaston 2000; Wilson 2011). Importantly, these mechanisms are not mutually exclusive (Faulks et al. 2015) and a common thread connecting these hypotheses, explicitly or implicitly, is the degree of spatial aggregation at multiple spatial scales (Storch et al. 2008). Despite this well-established theory there are relatively few detailed empirical and mechanistic examples of intraspecific AORs that account for time and space (Borregaard & Rahbek 2010; Faulks et al. 2015), especially for rare and/or declining species which may not follow the positive abundance-occupancy paradigm (e.g Freckleton et al. 2005; Webb et al. 2007). Furthermore, species that occur at low abundance tend to be narrowly distributed and face what has been termed 'double jeopardy', whereby extinction risk increases due to the chance of local stochastic events affecting entire populations (Gaston 1998).

Patterns in resource availability (e.g. food) in dynamic systems are often spatially autocorrelated, causing nomads to undergo dynamic changes in spatial aggregation (Webb et al. 2014). For example, when resources are spatially widespread, populations may expand their geographic range to exploit current conditions. Likewise, patches of abundant resources may result in high densities (or aggregations) of individuals. In times of poor resource availability, populations may experience resource bottlenecks whereby carrying capacity is exceeded or animals may be forced into low quality habitats that under better conditions would not be occupied (Manning et al. 2007).

The effect of food limitation may be further compounded when species require other resources to co-occur. For example, if the deterministic factor of the AOR is food, but if other required resources (e.g. nesting sites) are limited where food is abundant, this may have overall consequences for carrying capacity (fig. 1). Conversely, where nest sites are abundant food limitation may similarly constrain carrying capacity. When both resources are abundant

(relative to population size) individuals may be released from resource bottlenecks (fig. 1). Understanding dependencies between different system states and variation in the AOR may provide critical information to evaluating changes in carrying capacity and vital rates over time.

Because of the mobility and specialized needs of many nomads, models describing AORs where local densities are a direct function of habitat suitability or resource availability (eg. Brown et al. 1984; Holt et al. 1997) may not adequately describe the nature of relationships, or the underlying ecological processes that give rise to them. Similarly, the effects of dispersal ability and habitat patchiness on the AOR that apply to less mobile species (Freckleton et al. 2005) are likely to be much weaker, or absent for nomads.

We hypothesise that for nomadic species like the swift parrot, abundance-occupancy relationships are likely to be highly variable because of dynamic spatiotemporal variation in food availability. Using data collected from a multi-year population monitoring study we predict that: (1) the temporal AOR is likely to be negative at the population level, and attributable to the decrease (or increase) in local abundances in response to increasing (or decreasing) food resources, and, (2) the relationship between abundance and occupancy probabilities is likely to be positive, but varies over time with the availability and spatial configuration of food. In the context of previous studies examining AORs, our study provides novel empirical insights into the causal mechanisms of AORs for nomadic species facing multiple threats in dynamic systems, and the likely consequences for population dynamics and vital rates.

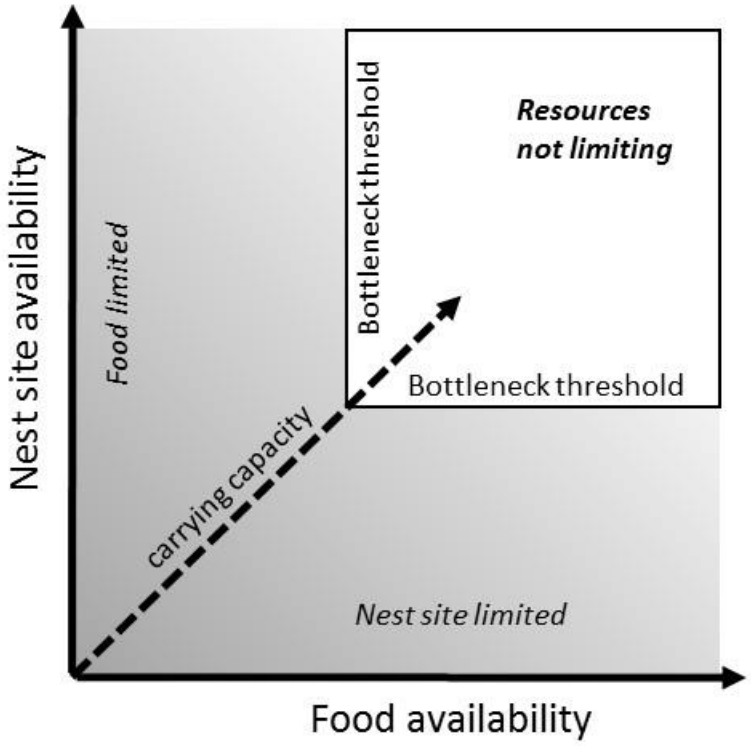

Fig 1. A conceptual model of how the relative availability of functional habitats may affect carrying capacity for a species requiring two functional habitats to co-occur (e,g, food and nesting). The x and y axes indicate increasing food and nest site availability, respectively; the dashed arrow indicates carrying capacity, whereby nest sites are limiting below the arrow and food is limiting above the arrow. Once beyond the 'bottleneck threshold' (white box) resources are not limiting relative to population size. For nomadic species in dynamic environments system states can vary over relatively short time frames where one (or more) resources may be limiting.

MATERIAL AND METHODS

Empirical data and study species

The swift parrot breeds only in Tasmania, Australia where it is threatened by habitat loss and an introduced nest predator (Heinsohn et al. 2015; Webb et al. 2017). During breeding the species depends on the flowering of two eucalypt tree species for food, but flowering patterns are dynamic and spatially structured (Webb et al. 2014). Underlying this spatiotemporal variation in flowering, the density and distribution of food trees is also highly fragmented due to both natural and anthropogenic processes (APPENDIX A, fig. A1). As a result, swift parrots undergo extreme variation in the location of occupied habitat and the degree of spatial aggregation over time (Webb et al. 2014; Webb et al. 2017), resulting in significant temporal variation in the availability of both foraging habitat (APPENDIX A, fig. A1*a-g*) and nesting habitat (tree cavities that take >150 years to develop) (Webb et al. 2017).

Swift parrot presence-absence data were collected during the early breeding season (i.e. October) when the species has settled to nest, allowing their breeding distribution to be measured in that year (Webb et al. 2017). Between 2009 and 2015 several hundred fixed sites were surveyed (mean number of sites surveyed each year 942, SD 105) across their breeding range (approximately 10,000 km^2). A site was defined as a 200 m radius around a fixed point and surveyed using repeated site visits (2-5 visits per site). Variation in the number of site visits was due to access to remote or private land sites, and deliberately focussing more effort in regions where birds were present in order to better estimate detectability at a site (given presence) (see Specht et al. 2017). Counts of swift parrots were conducted at the same time (and spatial scale); here we use the maximum count from each site for each year as a measure of site abundance. Flowering of food trees was also recorded during bird surveys to provide a measure of food abundance. Flowering was scored on a scale of 0 to 4, where 0= none, 1=

light, 2= moderate, 3= heavy and 4= very heavy flowering. Each site was assigned the flower score of the heaviest flowering tree (see Webb et al. 2014 for further details).

To examine AORs of swift parrots over 7 years across their breeding range we used the raw data outlined above and occupancy model predictions from Webb et al. (2014 & 2017), with an additional year of data. These zero-inflated binomial models account for imperfect detection, food availability and spatial autocorrelation through the inclusion of a spatially explicit covariate. Models were implemented in a Generalized Additive Model (GAM) framework in R-package mgcv (Wood 2004) utilising the EM Algorithim (*sensu* Webb et al. 2014).

Prediction 1: negative temporal abundance-occupancy relationship and food availability

We predicted that a negative temporal AOR exists at the population level for the swift parrot, and is attributable to a decrease in local abundances in response to increasing spatial extent of food resources, or vice versa. To examine this we tested for a correlation between local mean abundance and the number and proportion of occupied sites in each year of the study using Pearson's product-moment correlation. Local mean abundance was the mean count at all sites where the species was detected, a commonly used abundance metric to investigate AORs (Webb et al. 2012). The proportion of occupied sites was calculated by dividing the number of sites where the species was detected by the total number of sites surveyed. We then tested for a relationship between the proportion of occupied sites and the proportion of sites with high densities of birds, following a similar approach to Conrad et al. (2001). Here, the term

'high density' refers to unusually large aggregations of birds at a single site, and in this context high density sites were defined as those where >10 birds were recorded, noting that 10 birds exceeds the highest local mean abundance estimate over the seven years (table 1). We then summed the number of birds counted at high density sites and calculated the proportional contribution of these sites to the total count of birds each year. Again, we tested for a correlation between the annual proportion of occupied sites and the annual value of this metric.

To examine if the temporal AOR was influenced by food availability we used the proportion of sites with a flower score of two (i.e. moderate flowering) or greater in each year as an index of food abundance (hereafter: flowering sites). We used a flower score of two or greater because the mean flower score of occupied sites over the seven years was 2.15 (S.D. 0.37). We tested for a correlation between our index of food availability and the proportion of occupied sites, local mean abundance, and metrics derived from high density sites. All analyses were implemented in R (R Development Core Team 2016).

Prediction 2: positive but variable relationship between abundance and the probability of occupancy

Site scale

We predicted that a positive relationship between abundance and the probability of occupancy exists across a range of spatial scales, but the nature of the relationship varies over time with the availability and spatial configuration of food. To examine the relationship at the site-scale we used GAMs in R-package mgcv (Wood 2004). We fitted models with $ABUNDANCE_{site}$ (maximum count at each site) as the response variable, site-level $OCCUPANCY_{site}$ estimates (Webb et al. 2014, 2017) as a continuous predictor variable

(grouped by *YEAR*) and *YEAR* as a factor (which we considered a surrogate for annual variation in food availability). The inclusion of $OCCUPANCY_{site}$ as a smoothed term in models accounted for non-linear relationships and we used a negative binomial distribution to account for overdispersion in the data (Wood 2004).

Landscape scale

The scale of spatially structured flowering events is generally much larger than the scale of the sites surveyed (0.125 km^2), and swift parrots can forage several kilometres from their nest (Webb et al. 2014). Therefore, we also examined the relationship at a broader and more ecologically relevant landscape scale. To achieve this we interpolated annual occupancy model predictions ($OCCUPANCY_{land}$) using kriging with a cell size of 2.25 km^2, search radius 5 km and a spherical semivariogram model (using ArcMap 10.2, *sensu* Webb *et al*, 2014). Using the same cell size and search radius we also interpolated observed parrot abundances ($ABUNDANCE_{land}$) over the same time period, resulting in an annual mean of 4517 (S.D. ± 424) comparable cells across the 7 years. We used similar models to the site-scale analyses, fitting negative binomial GAMs with $ABUNDANCE_{land}$ from each cell as the response variable. Again, *YEAR* was included as a factor and a smoothed $OCCUPANCY_{land}$ term (grouped by *YEAR*) was used to account for non-linear relationships.

For both the site-scale and landscape-scale analyses, all three combinations of the two covariates were fitted:

i) *ABUNDANCE ~YEAR*,

ii) *ABUNDANCE ~OCCUPANCY* (grouped by *YEAR*) and

iii) *ABUNDANCE ~ OCCUPANCY* (grouped by *YEAR*) + *YEAR*

In models with the occupancy term, both smoothed and linear terms were tried. AICs were used to choose the best model overall (APPENDIX B, table A1).

RESULTS

Prediction 1: negative temporal abundance-occupancy relationship and food availability

Local mean abundance was significantly and negatively correlated with the proportion of sites occupied ($p < 0.01$; Pearson's $r = -0.92$, table 1), supporting the existence of a negative temporal AOR (fig. 2a). The proportion of occupied sites was significantly and negatively correlated with the proportion of high density sites ($p = 0.016$; Pearson's $r = -0.85$) and the proportional contribution of counts from high density sites to the total count of birds each year ($p < 0.01$; Pearson's $r = -0.96$) (fig. 2b).

The proportion of sites with good food availability (i.e. flower score of 2 to 4) was positively and significantly correlated with proportion of occupied sites each year ($p < 0.01$, Pearson's $r = 0.90$), but negatively correlated with local mean abundance ($p < 0.05$, Pearson's $r = -0.77$). Food availability was significantly and negatively correlated with the proportional contribution of counts from high density sites to the total count ($p = 0.015$, Pearson $r = -0.85$), but not with the proportion of sites defined as high density ($p = 0.082$, Pearson $r = -0.70$).

Prediction 2: positive but variable spatial abundance-occupancy relationship

The relationship between abundance and the probability of occupancy was positive and variable at both the site and landscape-scales (figs. 3 & 4). At both scales the best models (based on AIC scores) included the smoothed *OCCUPANCY* covariates (grouped by *YEAR*) and *YEAR* as a factor (APPENDIX B, table S1). All AORs were non-linear and varied between years (APPENDIX B, table S2; figs. 3 & 4). At the site-scale, the shape of the relationship was similar in 2010, 2012, 2013 and 2015. In contrast, for 2009, 2011, 2014 the

shape and/or magnitude of the relationship differed markedly from one another, and from the other more consistent years (figs. 3 & 4). The relationship was strongest in 2009 and 2014, particularly at higher occupancy values (eg. 0.9 - 1.0). The relationship was closest to linear in 2009, but appeared to plateau in 2011 with little increase in abundances beyond occupancy of 0.4. These differences among years (i.e. 2009, 2011 and 2014) at high occupancy values (eg. 0.8 – 1.0) were even more pronounced at the landscape-scale with steep upward trends in 2011 and 2014 (fig. 4). The strength of the relationship was again more moderate in 2010, 2012, 2013 and 2015. Importantly, the clear differences in the shape and strength of the relationships in the other years corresponded to lower proportions of occupied sites and 'flowering sites', and a higher proportion of the total count attributable to high density sites (table 1, fig. 2b). Furthermore, differences among years also corresponded to annual variation in the spatial configuration of food (see APPENDIX A, fig. A1*a-g*, discussed below).

Table 1. Summary of swift parrot occurrence, abundance and food availability over 7 years. Standard errors for local mean abundance is reported in parentheses. High density sites were those with >10 individuals recorded.

	Year						
	2009	2010	2011	2012	2013	2014	2015
Occupied sites	66	151	127	151	156	87	136
Total sites surveyed	755	834	996	989	982	1045	990
Proportion of sites occupied	0.087	0.181	0.127	0.153	0.159	0.083	0.138
Total count	526	619	693	665	556	602	688
Local mean abundance	7.8 (1.1)	4.3 (0.3)	5.5 (0.7)	4.4 (0.4)	3.6 (0.3)	6.8 (1.2)	5.1 (0.5)
No. of high density sites	20	12	16	13	11	16	22
Proportion of occupied sites with high density	0.303	0.079	0.126	0.086	0.071	0.184	0.162
Total count from high density sites	382	192	346	224	174	401	350
Proportion of total count recorded at high density sites	0.726	0.310	0.499	0.337	0.313	0.666	0.509
Proportion of sites with flower score ≥ 2	0.139	0.393	0.150	0.233	0.309	0.110	0.178

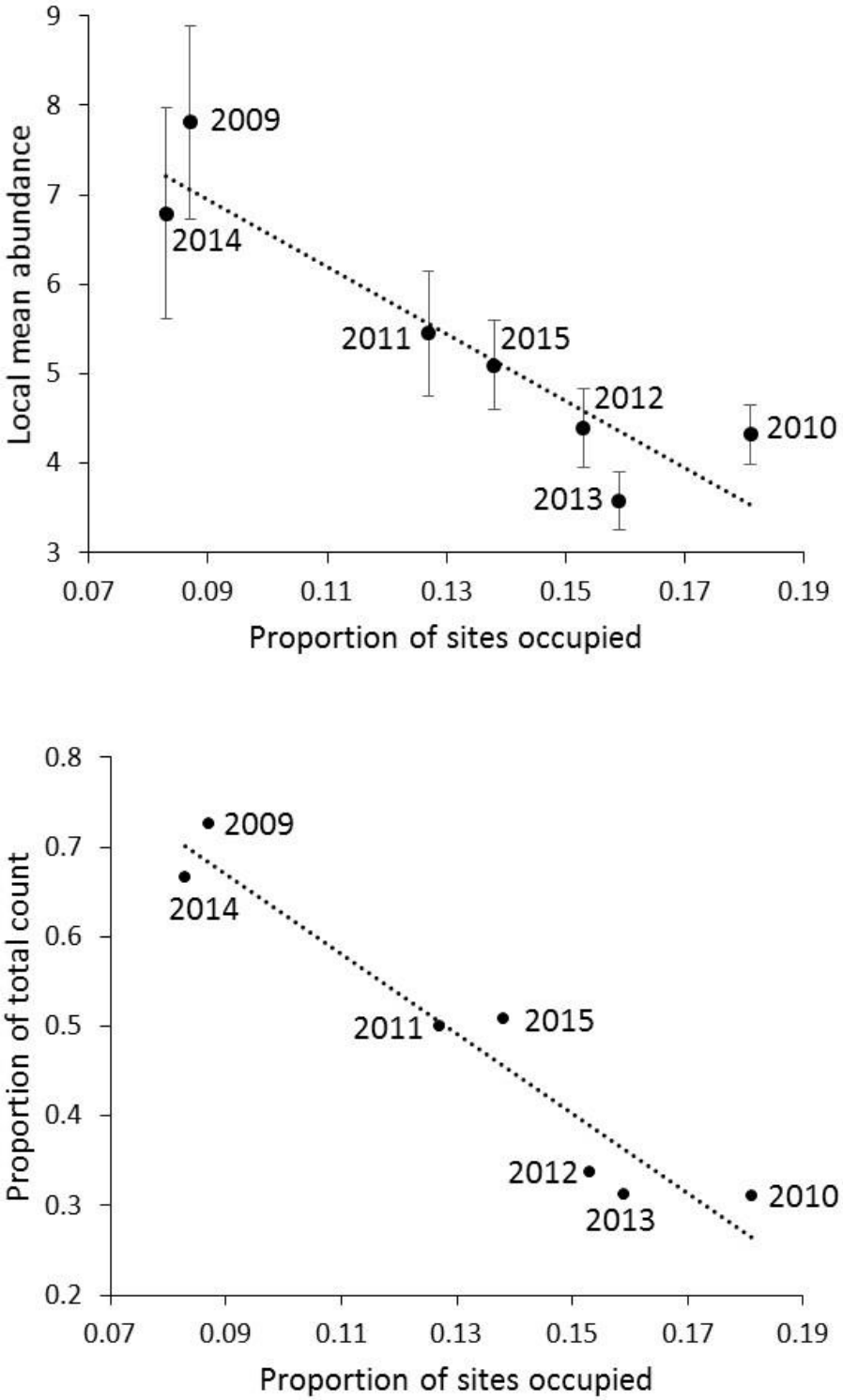

Figure 2. Proportion of occupied sites plotted against (a) mean swift parrot abundance and (b) proportional contribution of counts from high density sites to the total count of birds each year; error bars represent standard errors; dotted line represents linear trendline.

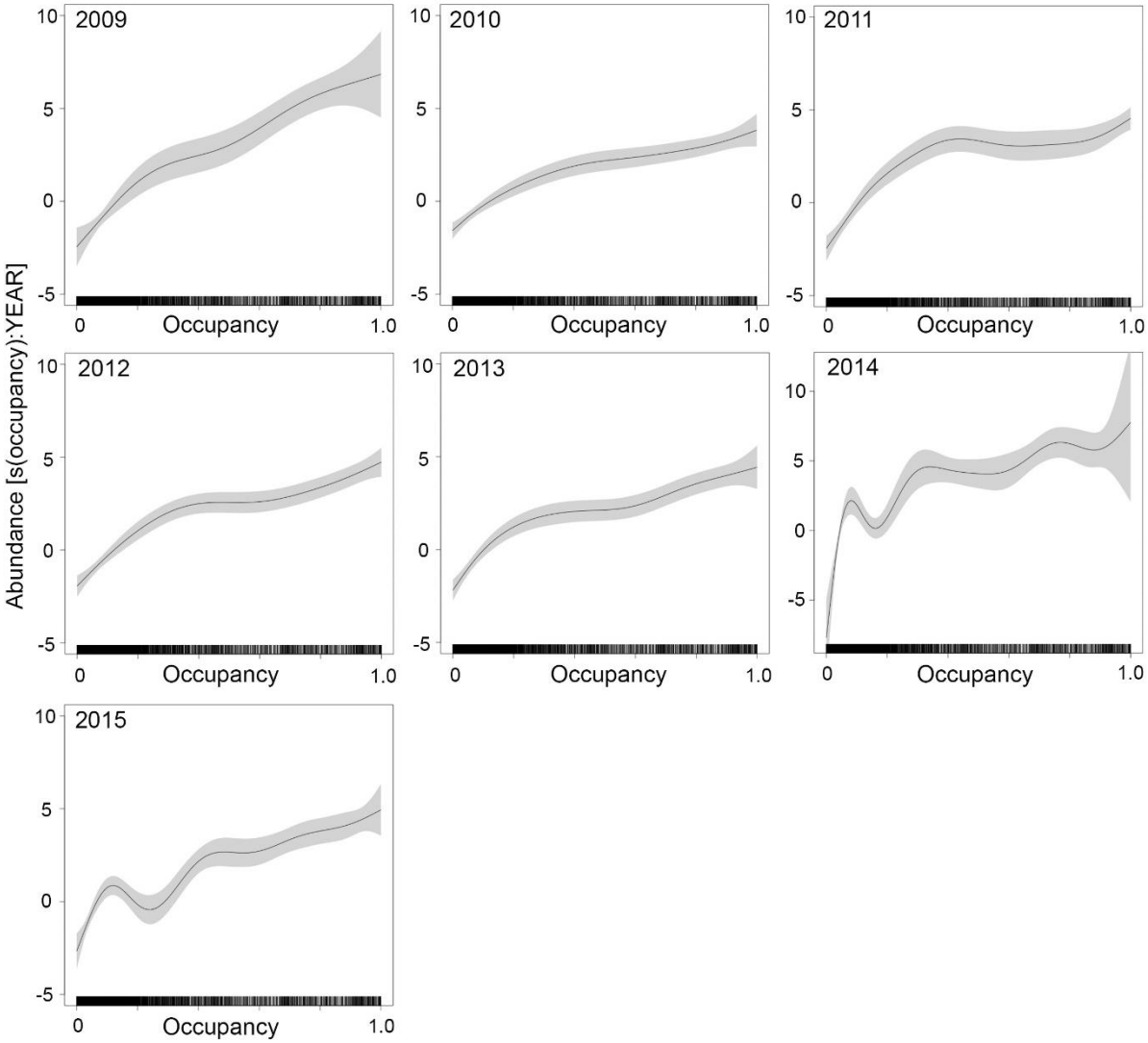

Figure 3. The smoothed occupancy function plotted against linear occupancy showing the shape of the abundance-occupancy relationship at the site-scale with *YEAR* as a factor; based on the model $ABUNDANCE_{site} \sim s(OCCUPANCY_{site}, by=YEAR) + YEAR$.

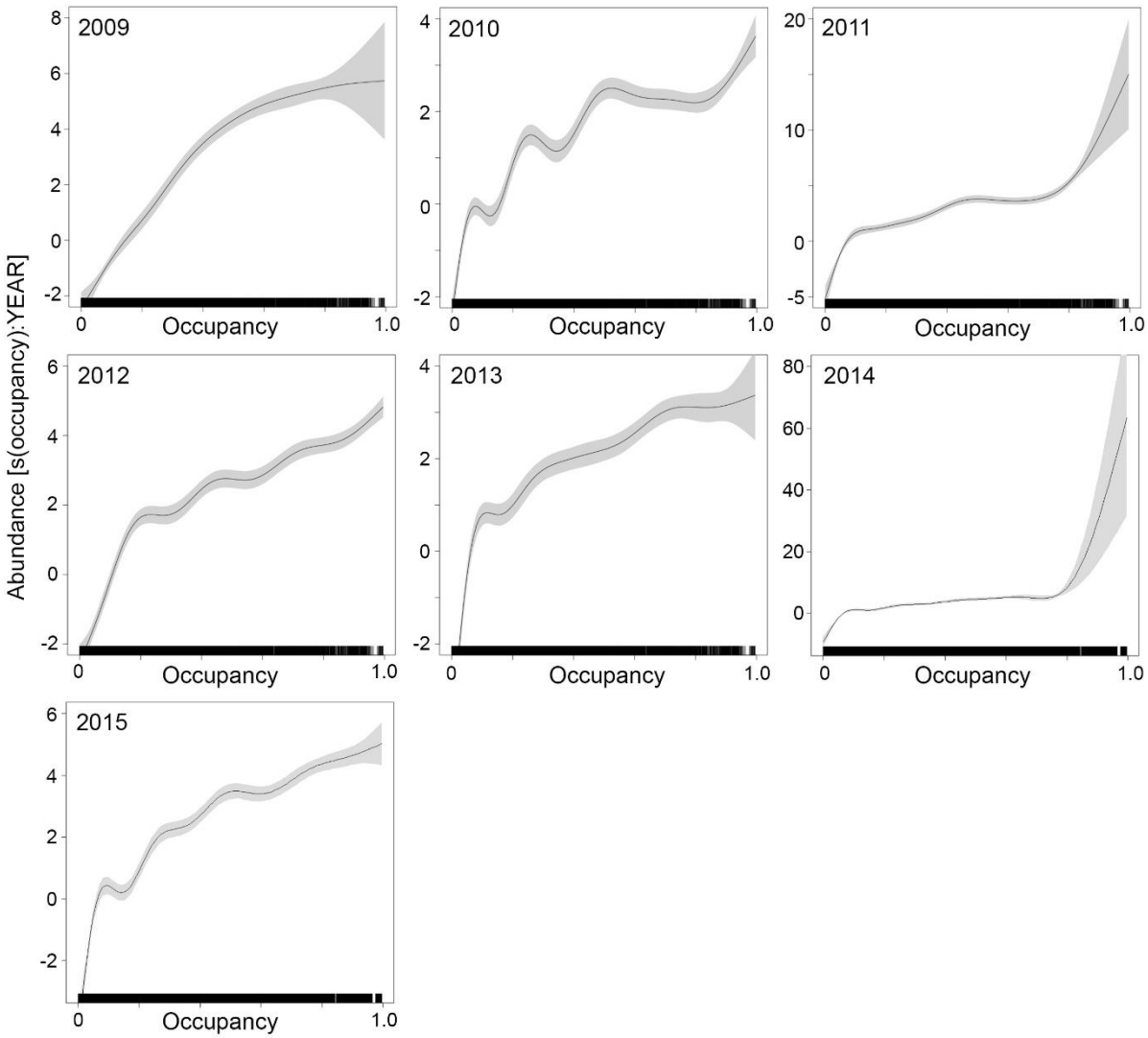

Figure 4. The smoothed occupancy function plotted against linear occupancy showing the shape of the abundance-occupancy relationship at the landscape-scale with *YEAR* as a factor; based on the model $ABUNDANCE_{land} \sim s(OCCUPANCY_{land}, by=YEAR) + YEAR$; **note different scales on the y-axes**.

DISCUSSION

Our findings provide a rare example of spatial and temporal dynamics in the abundance-occupancy relationship for a highly mobile nomadic migrant and is underpinned by a clear ecological mechanism. Our predictions of a negative temporal AOR and a positive but variable spatial relationship were both supported by the data. Our results provide strong evidence that the AOR is primarily influenced by varying degrees of spatial aggregation (Freckelton et al. 2006; Storch et al. 2008; Webb et al. 2012) which, for the nectar-dependent swift parrot, is caused by the dynamic and spatially structured flowering patterns of food trees (Webb et al. 2014 & 2017; also see APPENDIX A for annual flowering conditions). Our results are important because they provide i) empirical support for previous hypotheses on the causal mechanisms of AOR relationships, and ii) improved understanding of the ecological consequences of these relationships for species relying on dynamic systems.

The temporal AOR shows that as the proportion of occupied sites decreases, local mean abundance increases with a corresponding increase in variation around the mean (fig. 2a). This results in a greater proportion of the total count being attributable to high density sites (fig. 2b) and a higher degree of aggregation. In turn, this was reflected by changes in the shape of the relationship between abundance and the probability of occupancy between years (figs. 3 & 4), which are most pronounced at the more ecologically relevant landscape scale. The clear differences in the shape and strength of the landscape-scale relationship expressed in 2009, 2011 and 2014 (fig. 4) corresponded to very poor flowering years with fewer flowering sites (table 1). The location and degree of aggregation of the species may make it more or less susceptible to non-habitat related threats (Buckley et al. 2017), resource bottlenecks (Runge et al. 2014) and ongoing habitat loss (Webb et al. 2017). This has interesting implications in the context of 'double jeopardy' (Gaston 1998). That is, rather

than abundance decreasing with fewer occupied sites (or range size) it increases, but this still increases the risk of the entire population being exposed to a specific threatening process.

Changes in the relative availability of functional habitats (Webb et al. 2017) as a result of flowering patterns (fig. 1 & APPENDIX A) likely influences the AOR. For example, in 2014 small spatially aggregated patches of food (see APPENDIX A, fig. A1*f*) coupled with other spatially isolated sites with flowering trees, resulted in a dramatic reduction in the availability of nesting habitat (Webb et al. 2017). Under these conditions, habitat limitation may decouple the association between the AOR and habitat quality, whereby carrying capacity is reached or exceeded at marginal sites, with remaining individuals unable to breed or forced into even less suitable locations (i.e. isolated occurrences of food). At the landscape scale in both 2011 and 2014, this likely causes both plateaus in the AOR at mid-range occupancy values, and the steep increases at high occupancy values (>0.8). By contrast, in years when food was more abundant (i.e 2010, 2012, 2013 & 2015; APPENDIX A, fig. A1*a-g*) the shape of the relationship tended to be more similar, with smaller increases in abundance across a broad range of occupancy values at both spatial scales. Thus, more widespread food results in birds being more dispersed and less spatially aggregated at the scales examined in this study (i.e. site and landscape), and an overall weaker relationship between abundance and occupancy.

Quantifying the strength and shape of the AOR for species with dynamic distributions is of particular importance for understanding spatiotemporal changes in local density and assessing habitat quality (figs. 3 & 4). Because the relationship varied between years, was scale dependent, and generally non-linear, our results suggest that for nomadic species such as the swift parrot, incorporating abundance data into dynamic distribution models will be crucial to evaluating changes in carrying capacity (Hobbs and Hanley 1990; McLeod 1997;

Howard et al. 2014), exposure to other threats (McLoughlin et al. 2010) and ultimately vital rates of the population (Heinsohn et al. 2015).

Our results have important implications for evaluating the relative availability of different functional habitats for the swift parrot (food and nesting sites), which can vary markedly between years (Webb et al. 2017). While food is the primary driver of the AOR, it is possible for one or both functional habitats to be limiting in a given year, with overall consequences for carrying capacity (fig. 1). Similar patterns and consequences are likely for many other nomads that require co-occurrence of specific resources during their life cycle, both in Australia and in other parts of the globe.

In the context of previous hypotheses regarding the mechanisms driving AORs, the causal mechanisms of the swift parrot AOR are most likely a combination of (1) resource use and availability (Brown 1984; Hanski et al. 1993), (2) habitat dispersal (Venier and Fahrig 1996; Freckleton et al. 2005) and (3) density-dependent habitat selection (O'Conner 1987; Wheatley et al. 2002) (also see Table 1 in Borregaard and Rahbek 2010). When flowering trees were more abundant and widespread the population dispersed and occupied more sites (i.e. mechanisms 1 & 2). When the distribution of food contracted to smaller areas, so did the swift parrot population. If this results in high individual density and food or nest site limitation (fig. 1), intra- and possibly interspecific competition may force birds into less suitable habitats (i.e. mechanisms 1 & 3) (McLoughlin et al. 2010). The relative importance of each mechanism likely depends on the state of the system (i.e. the spatial configuration and availability of food; table 1 and APPENDIX A, fig. A1*a-g*), and each is critical to understanding how population dynamics scale temporally and spatially.

These empirical insights highlight how the variable distributions of nomads and degrees of spatial aggregation can affect the AOR. Because swift parrots are highly mobile the potential

limiting effects of dispersal and colonisation, experienced by less mobile species (Freckleton et al. 2005), on the AOR may be negated. Hence high abundances can potentially occur at locations where habitat quality is high or low (and abundant or limiting), depending on overall resource availability. Thus, high densities of individuals does not necessarily equate to high quality habitat (Van Horne 1983; Mosser et al. 2009) or areas of higher productivity or reproductive success (Thuiller et al. 2014).

By incorporating information on the AOR for a highly mobile nomad we take a step towards better identifying fluctuations in carrying capacity and resource bottlenecks (e.g. Runge et al. 2016; Veloz et al. 2015), and interpreting dynamic distribution models. Other non-habitat related threats may underlie these resource driven processes (Bastille-Rousseau et al. 2016), and may act independently, or synergistically with resource availability. A good example is the spatially variable predation of swift parrot nests by an introduced predator, which usually results in nest failure and often death of the female (Stojanovic et al. 2014). Because resource selection does not appear to be influenced by this process, as has been demonstrated in other species (eg. Mao et al. 2005; McLoughlin et al. 2010), understanding spatiotemporal variation in both distribution and abundance is critical to estimating vital rates (Thuiller et al. 2014) and may also improve understanding of the complex variation in population-level effects of settlement patterns.

In this case, resource limitation may curtail the number of individuals that can nest, whereas nest predation regulates reproductive success and the number of nesting females killed. However, if resource limitation and predation co-occur, then predation impacts may be offset by fewer females being killed because fewer nests are initiated (fig. 1). Conversely, resource abundance (where nest predation rates are high) may result in high female mortality, or high reproductive output where predators are absent or at low densities. Merging spatial and temporal knowledge of the AOR with the cumulative effects of resource availability (Webb

et al. 2017; Stojanovic et al 2015) and variable predation rates on reproductive output may provide significant improvements to modelling population viability over time (Heinsohn et al. 2015).

Population level monitoring of nomads is often judged to be too difficult or resource intensive, particularly if the objective is to collect abundance data. Yet, significant conservation resources are often routinely directed towards implementing on ground actions for these species without an adequate understanding of their spatial ecology (eg. offsets, habitat restoration, and predator control). Here we show that understanding the causal mechanisms of AORs for nomads, and how they change over time, may provide an empirical means to detect changes in population size and guide conservation planning. Despite the dynamic nature of key locations for many nomads, occurrence models have already provided crucial information for setting conservation priorities for the swift parrot (Webb et al. 2014; Webb et al. 2017), and continued monitoring is beginning to reveal patterns of reuse of particular regions. By incorporating knowledge of how the AOR varies over time we take a step towards better identifying (and protecting) high priority sites (e.g. Runge et al. 2015; Veloz et al. 2015) and targeting specific management actions such as predator suppression. The success of similar studies will require the recognition that sampling intensively and extensively is critical to generate meaningful data for nomads. Such data are fundamental to identifying locations where the allocation of resources are most likely to have a positive effect, and to identify population level processes operating at different temporal and spatial scales.

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SUPPORTING INFORMATION

APPENDIX A

Fig. A1*a-g*. Interpolated flowering conditions in the swift parrot breeding range between 2009 and 2015.

APPENDIX B

Table A1. AIC scores for GAMs at the site and landscape-scales.

Table A2. Significance of smoothed occupancy terms from the best site-scale GAM and landscape-scale GAM.

REFERENCES

Bastille-Rousseau, G., Schaefer, J.A., Lewis, K.P., Mumma, M.A., Ellington, E.H., Rayl, N.D. et al. (2016). Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. *J. Anim. Ecol.*, 85, 445-456.

Blackburn, T.M., Cassey, P. & Gaston, K.J. 2006. Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *J. Anim. Ecol.*, 75, 1426-1439

Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *Q. Rev. Biol.*, 85, 3-25.

Brown, J.H. (1984). On the relationship beween abundance and distribution of species. *Am. Nat.*, 124, 255-279.

Buckley, S.M., Thurstan, R.H., Tobin, A. & Pandolfi, J.M. (2017). Historical spatial reconstruction of a spawning aggregation fishery. *Cons. Biol.*, DOI: 10.1111/cobi.12940

Collier, B.A., Groce, J.E., Morrison, M.L., Newnam, J.C., Campomizzi, A.J., Farrell, S.L. et al. (2012). Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: An example of an American warbler. *Divers. Distrib.*, 18, 158-167.

Conrad, K.F., Perry, J.N. & Woiwod, I.P. (2001). An abundance–occupancy time-lag during the decline of an arctiid tiger moth. *Ecol. Lett.*, 4, 300-303.

Cottee-Jones, H.E.W., Matthews, T.J. & Whittaker, R.J. (2016). The movement shortfall in bird conservation: accounting for nomadic, dispersive and irruptive species. *Anim. Conserv.*, 19, 227-234.

Dingle, H. (2008). Bird migration in the southern hemisphere: a review comparing continents. *Emu*, 108, 341-359.

Faulks, L., Svanbäck, R., Ragnarsson-Stabo, H., Eklöv, P. & Östman, Ö. (2015). Intraspecific Niche Variation Drives Abundance-Occupancy Relationships in Freshwater Fish Communities. *Am. Nat.*, 186, 272-283.

Freckleton, R.P., Gill, J.A., Noble, D. & Watkinson, A.R. (2005). Large-scale population dynamics, abundance–occupancy relationships and the scaling from local to regional population size. *J. Anim. Ecol.*, 74, 353-364.

Freckleton, R.P., Noble, D. & Webb, T.J. (2006). Distributions of habitat suitability and the abundance-occupancy relationship. *Am. Nat.*, 167, 260-275.

Gaston, K.J. (1998). Rarity as double jeopardy. *Nature*, 394, 229-230

Gaston, K.J. (1999). Implications of interspecific and intraspecific abundance-occupancy relationships. *Oikos*,

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000). Abundance–occupancy relationships. *J. Appl. Ecol.*, 37, 39-59.

Gaston, K.J., Quinn, R.M., Blackburn, T.M. & Eversham, B.C. (1998). Species-range size distributions in Britain. *Ecography*, 21, 361-370.

Gutiérrez, D., Harcourt, J., Díez, S.B., Gutiérrez Illán, J. & Wilson, R.J. (2013). Models of presence‚Äìabsence estimate abundance as well as (or even better than) models of abundance: the case of the butterfly Parnassius apollo. *Landscape Ecol.*, 28, 401-413.

Hanski, I., Kouki, J., & Halkka A. (1993). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, pp. 108–116.

He, F. & Gaston, K.J. (2000). Occupancy-abundance relationships and sampling scales. *Ecography*, 23, 503-511.

Heinsohn, R., Webb, M.H., Lacy, R., Terauds, A., Alderman, R. & Stojanovic, D. (2015). A severe predator-induced decline predicted for endangered, migratory swift parrots (*Lathamus discolor*). *Biol. Conserv.*, 186, 75-82.

Holt, R.D., Lan-ton, J.H., Gaston, K.J. & Blackburn, T.M. (1997). On the relationship between range size and local abundance: Back to basics. *Oikos*, 78, 183-190.

Howard, C., Stephens, P.A., Pearce-Higgins, J.W., Gregory, R.D. & Willis, S.G. (2014). Improving species distribution models: The value of data on abundance. *Methods Ecol. Evol.*, 5, 506-513.

Kotze, D.J., Niemelä, J., O'Hara, R.B. & Turin, H. (2003). Testing abundance-range size relationships in European carabid beetles (Coleoptera, Carabidae). *Ecography*, 26, 553-566.

Kulhanek, S.A., Leung, B. & Ricciardi, A. (2011). Using ecological niche models to predict the abundance and impact of invasive species: application to the common carp. *Ecol. Appl.*, 21, 203-213.

Maclean, I.M.D., Wilson, R.J. & Hassall, M. (2011). Predicting changes in the abundance of African wetland birds by incorporating abundance–occupancy relationships into habitat association models. *Divers. Distrib.*, 17, 480-490.

Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M. et al. (2005). Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *J. Wildlife Manage.*, 69, 1691-1707.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering ecological dynamics in resource selection functions. *J. Anim. Ecol.*, 79, 4-12.

Mosser, A., Fryxell, J.M., Eberly, L. & Packer, C. (2009). Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecol. Lett.*, 12, 1050-1060.

Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, 94, 433-460.

O'Conner, R.J. (1987). Organisation of Communities: Past and Present (eds Gee, J.H.R. & Giller, P.S.). Blackwell Scientific Publications, Oxford, pp. 163-183.

R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria.

Runge CA, Tulloch A, Hammill E, Possingham HP, Fuller RA. 2015a. Geographic range size and extinction risk assessment in nomadic species. *Cons. Biol*., **29:**865-876.

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G. & Fuller, R.A. (2014). Conserving mobile species. *Front. Ecol. Environ.*, 12, 395-402.

Runge, C.A., Tulloch, A.I.T., Possingham, H.P., Tulloch, V.J.D. & Fuller, R.A. (2016). Incorporating dynamic distributions into spatial prioritization. *Divers. Distrib.*, 22, 332-343.

Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015b). Protected areas and global conservation of migratory birds. *Science*, 350, 1255.

Stojanovic, D., Terauds, A., Westgate, M.J., Webb, M.H., Roshier, D. & Heinsohn, R. (2015). Exploiting the richest patch has a fitness payoff for the migratory swift parrot. *J. Anim. Ecol.*, 84, 1194-1201.

Stojanovic, D., Webb, M., Alderman, R., Porfirio, L. & Heinsohn, R. (2014). Discovery of a novel predator reveals extreme but highly variable mortality for an endangered bird. *Divers. Distrib.*, 20, 1200-1207.

Storch, D., Šizling, A.L., Reif, J., Polechová, J., Šizlingová, E. & Gaston, K.J. (2008). The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecol. Lett.*, 11, 771-784.

Thuiller, W., Münkemüller, T., Schiffers, K.H., Georges, D., Dullinger, S., Eckhart, V.M. et al. (2014). Does probability of occurrence relate to population dynamics? *Ecography*, 37, 1155-1166.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *J. Wildlife Manage.*, 47, 893-901.

Veloz, S., Salas, L., Altman, B., Alexander, J., Jongsomjit, D., Elliott, N. et al. (2015). Improving effectiveness of systematic conservation planning with density data. *Conserv. Biol.*, 29, 1217-1227.

Venier, L.A. & Fahrig, L. (1996). Habitat availability causes the species abundance-distribution relationship. *Oikos*, 76, 564-570.

Verberk, W.C., van der Velde, G. & Esselink, H. (2010). Explaining abundance-occupancy relationships in specialists and generalists: A case study on aquatic macroinvertebrates in standing waters. *J. Anim. Ecol.*, 79, 589-601.

Webb, M.H., Terauds, A., Tulloch, A., Bell, P., Stojanovic, D. & Heinsohn, R. (2017). The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. *Conserv. Biol.*, DOI: 10.1111/cobi.12899

Webb, M.H., Wotherspoon, S., Stojanovic, D., Heinsohn, R., Cunningham, R., Bell, P. et al. (2014). Location matters: Using spatially explicit occupancy models to predict the distribution of the highly mobile, endangered swift parrot. *Biol. Conserv.*, 176, 99-108.

Webb, T.J., Freckleton, R.P. & Gaston, K.J. (2012). Characterizing abundance–occupancy relationships: there is no artefact. *Global Ecol. Biogeogr.*, 21, 952-957.

Webb, T.J., Noble, D. & Freckleton, R.P. (2007). Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *J. Anim. Ecol.*, 76, 123-134.

Weber, M.M., Stevens, R.D., Diniz-Filho, J.A.F. & Grelle, C.E.V. (2016). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, 39, 001-012.

Wilson, L.T. & Room, P.M. (1983). Clumping Patterns of Fruit and Arthropods in Cotton, with Implications for Binomial Sampling. *Environ. Entomol.*, 12, 50-54.

Wilson, P.D. (2011). The consequences of using different measures of mean abundance to characterize the abundance–occupancy relationship. *Global Ecol. Biogeogr.*, 20, 193-202, 44.

Wood, S.N. (2004). Stable and Efficient Multiple Smoothing Parameter Estimation for Generalized Additive Models. *J. Am. Stat. Assoc.*, 99, 673-686.

CONCLUSION

This study was developed to tackle the challenges inherent in devising an effective and informed conservation strategy for the critically endangered swift parrot. Many other species behave in similar ways, but due to statistical and logistic challenges, rigorous monitoring of their movements and ecology across multiple spatial scales has not been possible (Newton, 2006). This thesis provides the first population level assessment of a highly mobile nomadic species describing macroecological patterns in its variable geographic distribution and spatial dependency on food (i.e. flowering). I demonstrate that complex and spatiotemporally variable interactions between a difficult to study species and its food source can be effectively monitored and modelled to inform conservation management. Using existing and novel techniques, this research provides a platform that can be used to address common challenges facing sampling design and subsequent analyses that typically hamper monitoring and conservation planning for highly mobile, aggregating resource specialists.

By incorporating and contrasting information on abundance – occupancy relationships for a highly mobile nomad we take a step towards better identifying fluctuations in carrying capacity and resource bottlenecks (e.g. Runge et al. 2016; Veloz et al. 2015), and interpreting dynamic SDMs (Kalle et al. 2018). I show that understanding the causal mechanisms of abundance – occupancy relationships for nomads, and how they change over time, may provide an empirical means to understand changes in population size and range dynamics. I expect future empirical work may find comparable patterns to both nomadic and non-nomadic species that rely on aggregated but variable food sources such as nectarivores (Woinarski et al. 2000; Crates et al. 2017), frugivores (Boyle 2010, 2011; Kalle et al. 2018),

arid zone species (Runge et al. 2015a), or species exhibiting variable intraspecific movement strategies (Norbu et al 2017).

This research highlights the importance of accounting for spatial autocorrelation, not only for modelling the occurrence of spatially aggregating mobile species and the detection process, but also for understanding the links with abundance (Howard et al. 2014; Buckley et al. 2017). I demonstrate that devising a sampling design that captures the underlying spatial structure of the study system, combined with effective sampling protocols is fundamental to generating data that can inform conservation planning. Thus, without an understanding of the ecological mechanisms driving these processes in temporally variable and spatially structured systems misleading inferences can be drawn from monitoring data (Hui et al., 2010; Martin and Fahrig, 2012; Welsh et al., 2013). The approaches utilised in this study are likely to be particularly relevant to surveys conducted at large spatial scales in dynamic systems when few ecologically relevant covariates are available, or when the scale and/or influence of an environmental factor is unknown or varies across multiple temporal and spatial scales. Improving models and associated predictions in this way not only reduces uncertainty about the species distribution, but also provides land managers with more confidence to make decisions that affect other stakeholders.

My findings are critical to informing conservation planning decisions for the swift parrot because: (i) only a fraction of the breeding range is suitable (and occupied) in most years, (ii) the location of suitable habitat varies considerably between years; (iii) I identify focal regions for protection or restoration, (iv) I provide robust quantitative thresholds (e.g. occupancy probabilities and abundances) on which to base these decisions; (iv) they allow an assessment

of habitat availability to better inform the development of spatially explicit off-reserve conservation strategies and; (v) I provide an analytical framework for understanding population level processes into the future (e.g. carrying capacity and predation risk). Most importantly, I clearly identify areas of the breeding range that need to be managed in a way that provides enough habitat for the majority of the population to breed in a given year.

My research establishes baseline population data for the swift parrot and provides novel insights into population dynamics of nomadic migrants. Understanding the causal mechanisms of abundance-occupancy relationships for nomads may provide an empirical means to detect changes in population size and estimate population vital rates. For example, if the proportion of sites occupied decreases without a concomitant increase in local mean abundance or the number of high densities sites, it could imply a decrease in population size. Conversely, if the proportion of occupied sites increases and local mean abundance remains high, this could be attributable to a population increase. If the strength of the positive spatial abundance-occupancy relationship decreases while overall occupancy remains stable (or decreases), decreasing population size may again be implied. Incorporating abundance data into distribution models may be of particular importance where occupancy is high (and abundance more variable) as population change may be expressed through declining abundance at high density sites rather than overall occupancy. Similarly, change could also be expressed by presence-absence models converging with models of abundance over time. However, generation length may create lag times before declines are detected (Conrad et al. 2001).

Population level monitoring of nomads is often judged to be too difficult or resource intensive, particularly if the objective is to collect abundance data. Yet, significant

conservation resources are often routinely directed towards implementing on ground actions for these species (eg. offsets, habitat restoration, and predator control) without an adequate understanding of their spatial ecology. This research shows it is not only possible to undertake such studies, but that the results can yield rich ecological information to guide conservation planning. Moreover, I argue that in many cases, if sampling protocols adequately account for imperfect detection and spatial autocorrelation, this may also enable the collection and better interpretation of meaningful information on abundance.

Occurrence models have provided crucial information for setting conservation priorities for the swift parrot (Webb et al. 2014; Webb et al. 2017), and continued monitoring is beginning to reveal patterns of reuse of particular regions. By incorporating abundance-occupancy relationships we take a further step towards better identifying high priority sites (e.g. Runge et al. 2015; Veloz et al. 2015), fluctuations in carrying capacity, potential resource bottlenecks and exposure to other non-habitat related processes such as predation (McLoughlin et al. 2010).

Importantly, my thesis shows that locations of high predicted occupancy and/or abundance do not necessarily equate to areas of high quality habitat because of the spatial configuration of functional habitats and exposure to non-habitat related threats such as predation. This thesis delivers some of the first fundamental and quantitative insights into the spatial ecology of a highly mobile nomadic species that rely on variable environments, and provides guidance towards developing effective conservation plans for a group of species that is notoriously difficult to study and manage.

While I have focussed on a nomadic migrant, I suggest our results have broad applicability to understanding range dynamics and abundance – occupancy relationships for other species that rely on resources that vary in location and abundance (eg. frugivores, nectarivores and

arid zone species). Moreover, such patterns may occur at finer or larger scales than those explored in this study. Whether similar empirical evidence is demonstrated by future studies in other species will depend on the spatial and temporal scale of sampling in comparison to a species range dynamics. For example, if sampling is undertaken at finer resolutions than this study, and a species tracks spatially variable and aggregated resources at similar scales, comparable patterns may be observed (e.g. Guillaumet et al. 2017). Furthermore, the success of future studies will require the recognition that sampling intensively and extensively is critical to generate meaningful data for aggregating species with dynamic ranges. Such data will be fundamental to identify population level processes operating at different temporal and spatial scales.

Conservation planning for many migratory and nomadic species is at the frontier of conservation biology (Runge et al. 2015). Such is the severity of threats to migratory species that they are the subject of a dedicated international treaty, the Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention). However, while this and related legal instruments have improved the protection of species crossing international borders (Runge et al. 2014), there is often a legal void for species that are migratory or nomadic within national boundaries. Yet, even where there is legislation in place that *should* provide protection against for at risk species, and detailed knowledge of their conservation requirements, implementation of effective conservation action can still fail. One reason is that uncertainties about the impact of threats are potentially greater among migrant species. Migrants by definition occur at more sites than non-migratory species. Threatening processes may more readily identified and managed at the places where non migrants occur all year. As with legislation, however, excellent knowledge of threatening processes and how they can be managed does not guarantee action.

My thesis provides clear scientific evidence on how swift parrots use the landscape in time and space and allows the implementation of a more sophisticated spatially explicit management approach. Specifically my research was designed to (i) produce probabilistic spatial models of swift parrot occurrence and abundance, (ii) quantify variation in the spatial location and extent of occupied and available habitat, and (iii) measure variation in exposure of the population to sugar glider predation (Webb et al. 2014 & 2017).

In the context of continuing habitat loss and extreme nest predation two key questions for decision makers are: (i) is the evidence about swift parrot habitat requirements going to be incorporated into conservation planning, and (ii) will destruction of habitat then be halted? If habitat loss continues, it will now be for socio-economic reasons, not uncertainty about the species requirements. In a political/decision-making context several unresolved issues remain for swift parrot conservation planning, including habitat protection and nest predation. This thesis provides critical information to address these challenges in the future and guide the focus of conservation actions. Although resolving these issues is not a trivial matter in a political and logistical sense, there now exists a wealth of information on which to build sound evidence based conservation planning. Perhaps the biggest hurdle to swift parrot conservation is the political will to move beyond conservation paralysis in decision making and enact necessary actions to secure the species.

REFERENCES

Boyle, W. A. (2010). Does food abundance explain altitudinal migration in a tropical frugivorous bird? *Canadian Journal of Ecology*, 88, 204-213

Boyle, W. A. (2011). Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis. *Oikos*, 120, 1803-1816

Conrad, K.F., Perry, J.N. & Woiwod, I.P. (2001). An abundance–occupancy time-lag during the decline of an arctiid tiger moth. *Ecol. Lett.*, 4, 300-303.

Crates, R., Terauds, A., Rayner, L., Stojanovic, D., Heinsohn, R., Ingwersen, D., and Webb, M. (2017). An occupancy approach to monitoring regent honeyeaters. Journal of Wildlife Management, 81, 669-667

Guillaumet, A., Kuntz, W. A., Samuel, M. D., and Paxton, E. H. (2017). Altitudinal migration and the future of an iconic Hawaiian honeycreeper in response to climate change and management. *Ecological Monographs* 87, 410-428Hui, C., Veldtman, R., McGeoch, M. 2010. Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, 33, 95-102.

Martin, A. E., Fahrig, L. 2012. Measuring and selecting scales of effect for landscape predictors in species-habitat models. Ecological Applications 22, 2277-2292

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E. & Contasti, A.L. (2010). Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, 79, 4-12.

Newton, I., 2006. Advances in the study of irruptive migration. Ardea 94, 433-460

Norbu, N., Ugyen, M.C. Wikelski, and D.S., Wilcove. 2017. Partial altitudinal migration of the near threatened satyr tragopan Tragopan satyra in Bhutan Himalayas: implications for conservation in mountainous environments. *Oryx*, 51, 166-173.

Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P. & Fuller, R.A. (2015). Protected areas and global conservation of migratory birds. *Science*, 350, 1255.

Runge, C. A., A. I. T. Tulloch, H. P. Possingham, V. J. D. Tulloch, and R. A. Fuller. 2016. Incorporating dynamic distributions into spatial prioritization. *Diversity and Distributions*, 22, 332-343

Veloz, S., Salas, L., Altman, B., Alexander, J., Jongsomjit, D., Elliott, N. *et al.* (2015). Improving effectiveness of systematic conservation planning with density data. *Conservation Biology*, 29, 1217-1227.

Webb, M.H., Terauds, A., Tulloch, A., Bell, P., Stojanovic, D. & Heinsohn, R. (2017). The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems. *Conservation Biology*, DOI: 10.1111/cobi.12899.

Webb, M.H., Wotherspoon, S., Stojanovic, D., Heinsohn, R., Cunningham, R., Bell, P. *et al.* (2014). Location matters: Using spatially explicit occupancy models to predict the distribution of the highly mobile, endangered swift parrot. *Biological Conservation*, 176, 99-108.

Welsh, A. H., Lindenmayer, D. B., Donnelly, C. F. 2013. Fitting and interpreting occupancy models. *PLoS ONE* 8:e52015.

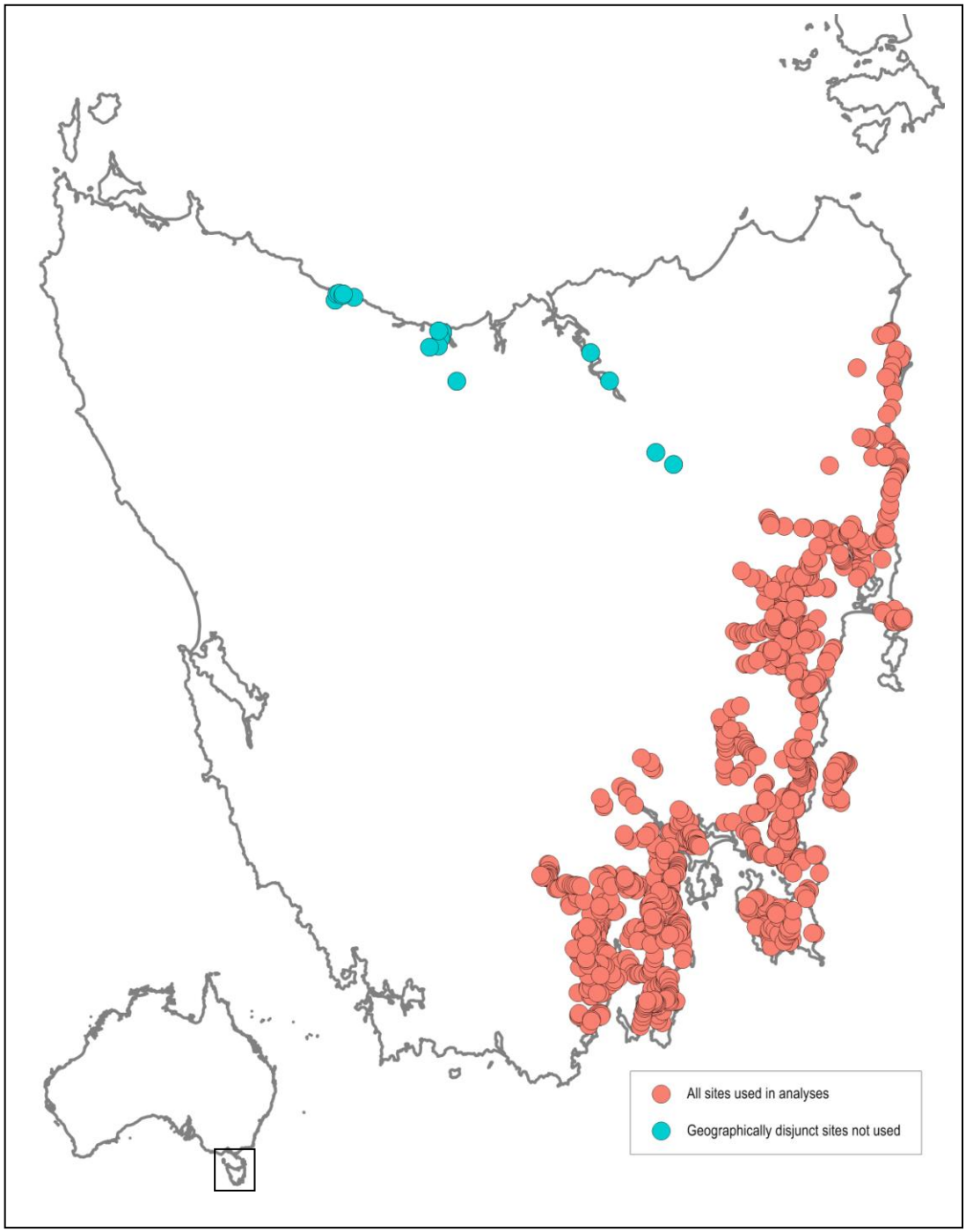
Woinarski J. C. Z., Connors, G. C., and Don F. (2000). Thinking honeyeater: nectar maps for the Northern Territory, Australia. *Pacific Conservation Biology*, 6, 61-80.

APPENDICES

Chapter 3 Appendix

Figure A1

All sites surveyed for swift parrots between 2009 and 2012. Represents total extent of known breeding range



Appendix A

Swift parrot sampling protocols, 2009-2012

Sampling sites were restricted to locations containing at least one *Eucalyptus globulus* or *Eucalyptus ovata*, which for the purpose of this study is defined as potential foraging habitat. The perimeter of a site was defined as a circle of 200 m radius around a fixed point. Site selection began at the nearest *E. globulus* or *E.ovata* tree with a DBH of greater >50 cm to a randomly selected point. All subsequent sites were selected by adhering to the following protocol: travel a minimum of 500 m along a road or track from the previous site, if at least one *E. globulus* or *E. ovata* is present then mark as the next site, if not, move to the nearest point that met this criterion and mark as the next site, and so on. This protocol was followed until, as much practicable, all roads/tracks with vehicular access within the study area were assessed, resulting in a wide range of forest types and including agricultural and urban landscapes. Sites were surveyed using repeated 5 minute visits (Table A1) to record the presence-absence of Swift parrots (seen or heard) at each site (presence). Birds observed flying over the site and not landing were not included.

Table 1. Mean number of 5 minute visits per site in each year.

Year	2009	2010	2011	2012
Mean number of visits (range)	2.56 (1-8)	2.48 (2-5)	2.55 (2-4)	2.06 (2-3)

Flowering intensity of the visible crown of *E. globulus* and *E. ovata* (flower) was scored from 0-4, where 0=none (<1% of crown), 1=light (<10% of crown), 2=moderate (10-40% of crown), 3=heavy (40-70% of crown), 4=very heavy (>70% of crown). The flowering intensity score of each site was recorded as the highest intensity flowering tree. To minimise the potential for temporal variation in detection probabilities due to changes in bird behaviour each survey was restricted to a short time period early in the breeding season (i.e. last three weeks in October) in 2009, 2010, 2011 and 2012.

Appendix B EM Algorithm

This appendix derives the EM algorithm for fitting zero-inflated Binomial models.

Zero-Inflated Binomial

Site occupancy data was collected by sampling a number of distinct sites repeatedly over time. At each site the number of occasions it was occupied was recorded. The model assumes that any site is either continuously occupied or unoccupied but detection is imperfect so that if the site is occupied there is no guarantee the target species will be sighted on any individual visit, and models the observed sightings with a zero-inflated Binomial distribution (Hall, 2000).

Suppose site i is visited n_i times, and sightings occur on y_i of these visits. Introduce a latent variable z_i that indicates whether a site is truly occupied, so that $z_i = 1$ if the site is occupied and $z_i = 0$ if the site is unoccupied. Then $y_i > 0$ implies $z_i = 1$ and $z_i = 0$ implies $y_i = 0$. If ψ_i is the probability that site i is occupied, and p_i is the conditional probability that a sighting will occur on any single occasion if the site is occupied, if it is assumed that sightings occur independently, the joint probability mass can be written as a zero-inflated Binomial

$$P(y_i, z_i|\psi_i, p_i) = [1 - \psi_i]^{1-z_i} \left[\psi_i \binom{n_i}{y_i} p_i^{y_i} (1 - p_i)^{n-y_i}\right]^{z_i}.$$

In turn, the probabilities of occupancy ψ_i and detection p_i can be related to arbitrary site specific covariates.

EM Algorithm

The EM algorithm (Dempster et al., 1977) is an iterative procedure for deriving maximum likelihood estimates in the presence of missing data. The zero-inflated Binomial model can be fitted with the EM algorithm by treating the the latent z_i as missing data.

Starting from an initial estimate $\theta^{(0)}$, the EM algorithm is an iterative two step process that generates a sequence of estimates $\theta^{(0)}, \theta^{(1)}, \theta^{(2)}, \ldots$ guaranteed to converge to the maximum likelihood estimate. The first or E step of the algorithm computes the expected log likelihood with respect to the missing data z, conditional on the observed data y and parameter estimates $\theta^{(i)}$ from the previous iteration

$$Q(\theta^{(i+1)}|\theta^{(i)}) = \mathrm{E}\{\log P(y, z|\theta)|y, \theta^{(i)}\},$$

where $P(y, z|\theta)$ denotes the joint distribution of the observed data and missing data given model parameters θ. The second or M step of the algorithm derives an improved estimate $\theta^{(i+1)}$ by maximizing $Q(\theta^{(i+1)}|\theta^{(i)})$ with respect to $\theta^{(i+1)}$.

To fit the zero-inflated model model by the EM algorithm, note that if $y_i > 1$

$$P(z_i|y_i > 0, \psi_i, p_i) = \begin{cases} 1 & \text{if } z_i = 1 \\ 0 & \text{if } z_i = 0 \end{cases}$$

but if $y_i = 0$

$$P(z_i|y_i = 0, \psi_i, p_i) = \alpha_i^{z_i}(1-\alpha_i)^{1-z_i}$$

where

$$\alpha_i = \frac{\psi_i(1-p_i)^{n_i}}{1-\psi_i+\psi_i(1-p_i)^{n_i}}.$$

E Step

The E step of the algorithm computes

$$Q(\{\psi_i\},\{p_i\};\{\psi_i'\},\{p_i'\}) = \sum_i Q_i(\psi_i, p_i; \psi_i', p_i')$$

where Q_i is the conditional expectation

$$Q_i(\psi_i, p_i; \psi_i', p_i') = \sum_{z_i} P(z_i|y_i, \psi_i, p_i) \log P(y_i, z_i|\psi_i', p_i')$$

and primes denote quantities estimated in the previous iteration. Direct calculation shows

$$Q_i(\psi_i, p_i; \psi_i', p_i') = \begin{cases} (1-\alpha_i')\log(1-\psi_i) + \alpha_i' \log\psi_i + \alpha_i' \log r_i & \text{if } y_i = 0, \\ \log\psi_i + \log r_i & \text{if } y_i > 0. \end{cases}$$

where

$$r_i = \binom{n_i}{y_i} p_i^{y_i}(1-p_i)^{n-y_i}$$

and hence the expression for Q can be separated into components in ψ_i and p_i

$$Q(\psi_i, p_i; \psi_i', p_i') = \sum_i Q_i^{(\psi)}(\psi_i; \psi_i') + \sum_i Q_i^{(p)}(p_i; p_i')$$

where

$$Q_i^{(\psi)}(\psi_i; \psi_i') = \begin{cases} (1-\alpha_i')\log(1-\psi_i) + \alpha_i' \log\psi_i & \text{if } y_i = 0, \\ \log\psi_i & \text{if } y_i > 0, \end{cases}$$

and

$$Q_i^{(p)}(p_i; p_i') = \begin{cases} \alpha_i' \log r_i & \text{if } y_i = 0, \\ \log r_i & \text{if } y_i > 0. \end{cases}$$

M Step

The M step of the algorithm maximises Q over the parameters $\{\psi_i\}$ and $\{p_i\}$, given the estimates $\{\psi_i'\}$ and $\{p_i'\}$ from the previous iteration. As Q can be separated into distinct components in $\{\psi_i\}$ and $\{p_i\}$, Q is maximized when $Q^{(\psi)}$ is maximized over $\{\psi_i\}$ and $Q^{(p)}$ is maximized over $\{p_i\}$.

Maximizing $Q^{(p)}$ over $\{p_i\}$ is a weighted Binomial regression with weights

$$w_i^{(p)} = \begin{cases} \alpha_i' & \text{if } y_i = 0, \\ 1 & \text{if } y_i > 0. \end{cases}$$

.

Writing $Q^{(\psi)}$ as

$$Q_i^{(\psi)}(\psi_i;\psi_i') = \begin{cases} \log(1-\psi_i) + \alpha_i' \log\frac{\psi_i}{1-\psi_i} & \text{if } y_i = 0, \\ \log(1-\psi_i) + \log\frac{\psi_i}{1-\psi_i} & \text{if } y_i > 0, \end{cases}$$

shows that maximizing $Q^{(\psi)}$ over $\{\psi_i\}$ is a Binomial regression for the response

$$z_i = \begin{cases} \alpha_i' & \text{if } y_i = 0, \\ 1 & \text{if } y_i > 0. \end{cases}$$

Covariates

The arguments of the previous sections also hold if the probabilities of occupancy ψ_i and detection p_i are expressed in terms of arbitrary site specific covariates. In particular, as the M step reduces to a pair of Binomial regressions in the covariates, the probabilities of occupancy ψ_i and detection p_i can be related to a set of covariates as standard parametric generalized linear model (GLM) or semi-parametric generalized additive model (GAM).

An R language implementation is given in Appendix D.

References

Dempster, A. P., Laird, N. M., and Rubin, D. B. (1977). Maximum Likelihood from Incomplete Data via the EM Algorithm. *Journal of the Royal Statistical Society Series B*, 39(1):1–38.

Hall, D. B. (2000). Zero-Inflated Poisson and Binomial Regression with Random Effects: A Case Study. *Biometrics*, 56(4):1030–1039.

Appendix C Simulation Testing

Appendix B demonstrated how the EM algorithm may be used to fit zero-inflated Binomial models. However, it is unclear if the zero-inflated occupancy model is identifiable when the probabilities of occupancy ψ and detection p are related to site specific covariates, or whether spatial variability in p will be confounded with variability in ψ. If the two components can not be clearly distinguished, there may be no value in fitting models that explicitly represent both detectability and occupancy.

The first part of this Appendix presents simulations to demonstrate that the model is indeed identifiable and variability in p can be distinguished from variability in ψ. The second part of this appendix qualitatively compares the fit of two models,

1. the zero-inflated Binomial model, and
2. a presence-absence Binomial model in which a site is considered occupied if the target species is sighted on any visit to the site.

Domain and Predictors

Data were simulated by generating N random sites uniformly distributed on the $[0,1] \times [0,1]$ square. Predictors were calculated for each site and used to construct the probability ψ of occupancy at a site, and the probability p of detecting the animal if the site is occupied. At least one survey was conducted at every site, and the number of additional surveys was assumed to be Poisson distributed.

Three of the predictors used in the simulations were smooth functions of space, two being sinusoids and the third a plane (see Figure 1)

$$\begin{aligned} f_1(x,y) &= \sin(\pi x)\sin(\pi y) \\ f_2(x,y) &= \sin(2\pi x)\sin(2\pi y) \\ f_3(x,y) &= 2(x - 1/2) \end{aligned}$$

while the remaining two predictors $f_4(x,y)$ and $f_5(x,y)$ were uniform random fields, so that at each point in the plane these functions represent a single draw from a simple uniform $\mathrm{U}(0,1)$ distribution.

Identifiability

The first part of this Appendix explores model identifiability.

GLM

First consider the case where both the ψ and p components of the model are fitted as parametric generalized linear models (GLMs).

Two simulations were conducted. In both cases, 25 replicate data sets of $N = 500$ sites where an average of 4 visits is made to each site were generated from a model with known coefficients. To these replicate data sets is fitted the

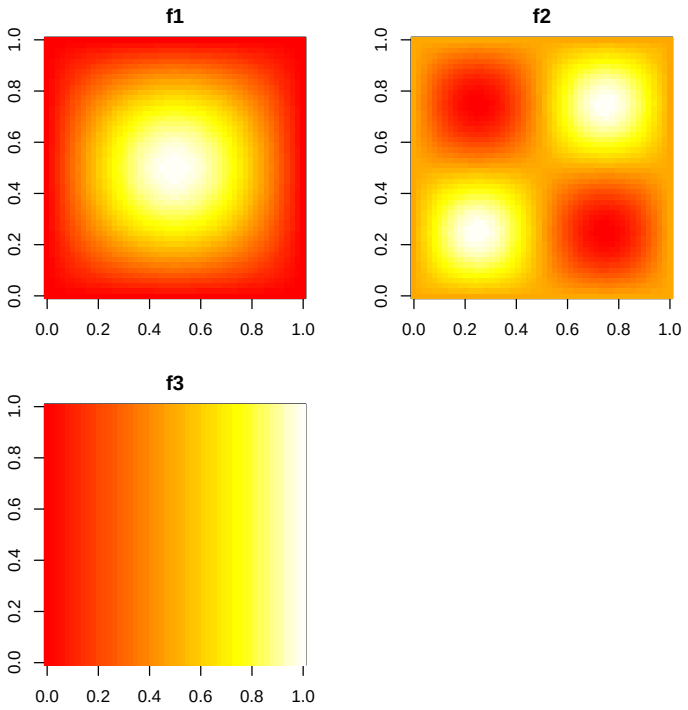


Figure 1: The three spatially smooth predictors.

model in which both the ψ and p components depend upon all 5 predictors

$$\log \frac{\psi}{1-\psi} = \alpha_0 + \alpha_1 f_1(x,y) + \alpha_2 f_2(x,y) + \alpha_3 f_3(x,y) + \alpha_4 f_4(x,y) + \alpha_5 f_5(x,y)$$
$$\log \frac{p}{1-p} = \beta_0 + \beta_1 f_1(x,y) + \beta_2 f_2(x,y) + \beta_3 f_3(x,y) + \beta_4 f_4(x,y) + \beta_5 f_5(x,y)$$

and $\alpha_0, \ldots, \alpha_5$ and $\beta_0, \ldots, \beta_5$ are regression coefficients to be estimated. Boxplots of the fitted coefficients are constructed to demonstrates the properties of the fit.

In the first simulation, data were simulated from a model in which ψ and p depend upon disjoint sets of predictors

$$\log \frac{p}{1-p} = 1/2 + 3/2\ f_1(x,y) + f_4(x,y)$$
$$\log \frac{\psi}{1-\psi} = 1/2 + 3/2\ f_2(x,y) + f_5(x,y).$$

Boxplots of the fitted coefficients are shown in Figure 2.

In the second simulation, data were simulated from a model in which the predictors upon which ψ and p depend are not disjoint

$$\log \frac{p}{1-p} = 1/2 + 3/2\ f_2(x,y) + f_4(x,y)$$
$$\log \frac{\psi}{1-\psi} = 1/2 + 3/2\ f_2(x,y) + f_5(x,y).$$

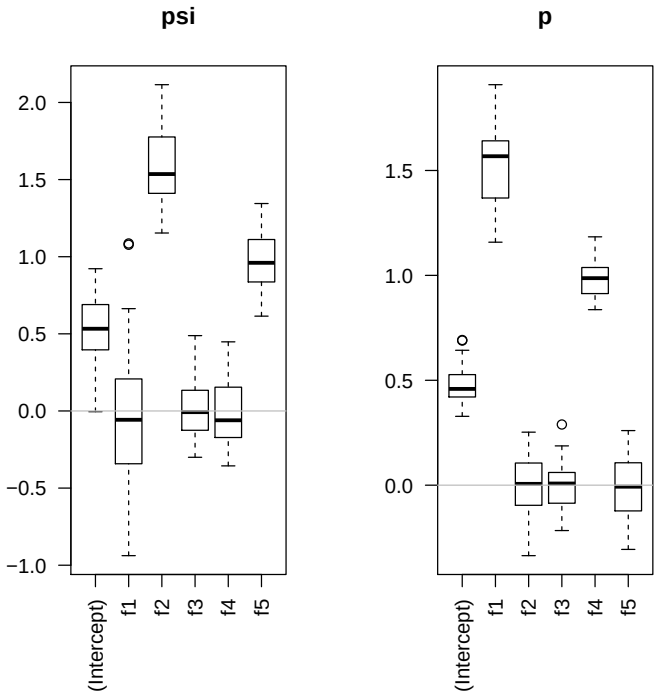


Figure 2: Boxplots of the fitted GLM coefficients when the predictors in the components of the true model are disjoint.

Boxplots of the fitted coefficients are shown in Figure 3.

In both cases the boxplots suggest that the model coefficients are estimable, and that variability in p can be distinguished from variability in ψ.

GAM

Now consider the case where both components of the model are fitted as generalized additive models (GAMs) with a two dimensional spatial smooth.

In this case four simulations were conducted. In each simulation, 5 replicate data sets of $N = 500$ sites where an average of 4 visits is made to each site were generated, and a semi-parametric model in which both the ψ and p components contain a smooth spatial term

$$\log \frac{\psi}{1-\psi} = \alpha_0 + g(x,y) + \alpha_4 f_4(x,y) + \alpha_5 f_5(x,y)$$
$$\log \frac{p}{1-p} = \beta_0 + h(x,y) + \beta_4 f_4(x,y) + \beta_5 f_5(x,y)$$

is fitted to each replicate data set. Here $g(x,y)$ and $h(x,y)$ are smooth spatial terms to be estimated, and α_0, β_0, α_4, β_4, α_5 and β_5 are regression coefficients to be estimated.

The first two simulations were based on the same models used in the previous section. Figure 4 shows the estimated $g(x,y)$ and $h(x,y)$ for each of the five

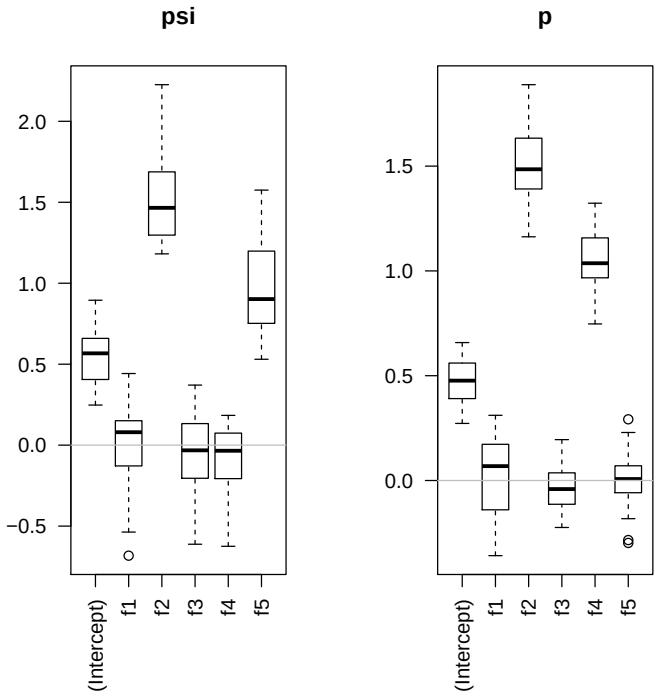


Figure 3: Boxplots of the fitted coefficients when the predictors in the two components of the model are not disjoint.

replicated datasets simulated from a model in which the two components of the model depend upon disjoint sets of predictors. Figure 5 shows the estimated $g(x, y)$ and $h(x, y)$ for each of the five replicated datasets simulated from a model in which the two components of the model depend upon sets of predictors that are not disjoint. In both simulations, the GAM model appears to be able to recover the spatial structure of the predictors.

In the third and fourth simulations, data was generated from a model in which only one of ψ or p has spatial structure.

In the third simulation, data were simulated from a model

$$\log \frac{p}{1-p} = 1/2 + 3/2\ f_2(x, y) + f_4(x, y)$$
$$\log \frac{\psi}{1-\psi} = f_5(x, y).$$

The estimated $g(x, y)$ and $h(x, y)$ for the five replicated datasets are shown in Figure 6.

In the fourth simulation, data were simulated from a model

$$\log \frac{p}{1-p} = f_4(x, y)$$
$$\log \frac{\psi}{1-\psi} = 3/2\ f_2(x, y) + f_5(x, y).$$

The estimated $g(x, y)$ and $h(x, y)$ for the five replicated datasets are shown in Figure 7.

In both Figure 6 and Figure 7, there is no indication of confounding of the two components of the model.

Model Comparison

In this section, data were generated from the zero-inflated occupancy model and the fit of two alternate models – the zero-inflated Binomial model and a presence-absence Binomial model – are qualitatively compared. In the presence-absence model, a site is considered occupied if the target species is observed on any visit to the site, and occupancy is modelled as a binary dichotomy regardless of the number of visits made to the site.

As in the previous section, both parametric (GLM) and semi-parametric (GAM) fits were considered.

GLM

First consider the case where both models are fitted as parametric generalized linear models (GLMs).

Three simulations were considered – one in which detection is perfect, on is which detection is poor, and one in which detection varies across the domain, while in all three ψ is modelled as

$$\log \frac{\psi}{1-\psi} = 3/2\ f_2(x, y) + f_5(x, y).$$

In all three simulations, 25 replicate data sets of $N = 500$ sites where an average of 4 visits is made to each site are generated from a model with known coefficients. Both models are fitted to the replicate data sets using all 5 available terms as predictors, and the fits compared.

In the first simulation, detection is perfect $p = 1$. Figure 8 show boxplots of the coefficients of both models. As would be expected, when detectability is perfect both models correctly identify factors influencing occupancy.

In the second simulation, detection is poor $p = 0.27$. Figure 9 show boxplots of the coefficients of both models. When detectability is poor, again both models correctly identify factors influencing occupancy.

In the third simulation, detectability varies across the domain

$$\log \frac{p}{1-p} = 3/2\ f_3(x, y).$$

Figure 10 show boxplots of the fitted coefficients for both models. When detectability varies over the domain, the zero-inflated model is able to separate factors influencing detectability and occupancy. Whereas the presence model still identifies all three of the covariates f_2, f_3 and f_5 as important, but effectively confounds the factor f_3 influencing detectability with those influencing occupancy.

GAM

Now consider the case where all three models are fitted as generalized additive models (GAMs) with a two dimensional spatial smooth, and detectability varies

across the domain

$$\log \frac{p}{1-p} = 2\ f_3(x, y)$$

In the first simulation, occupancy is modelled as

$$\log \frac{\psi}{1-\psi} = 3/2\ f_1(x, y),$$

while in the second

$$\log \frac{\psi}{1-\psi} = 2\ f_2(x, y).$$

Figures 11 and 12 show the fitted smooths for the two components of the zero-inflated model and the presence and sightings models.

In both case the zero-inflated model is able to separate factors influencing detectability and occupancy, whereas the presence model appears to conflate detectability and occupancy to some degree. In both Figures 11 and 12, the linear trend in detectability across the domain is reflected in the fitted smooth of the presence model.

Site Revisits

In part the success of the presence model can be attributed to the number of return visits made to each site.

Figure 13 shows the probability of at least one sighting in n visits assuming the target species is present as a function of p, the detection probability for a single visit. Even when the detection probability is low, the overall probability of at least one sighting becomes large provided the site is revisited often enough.

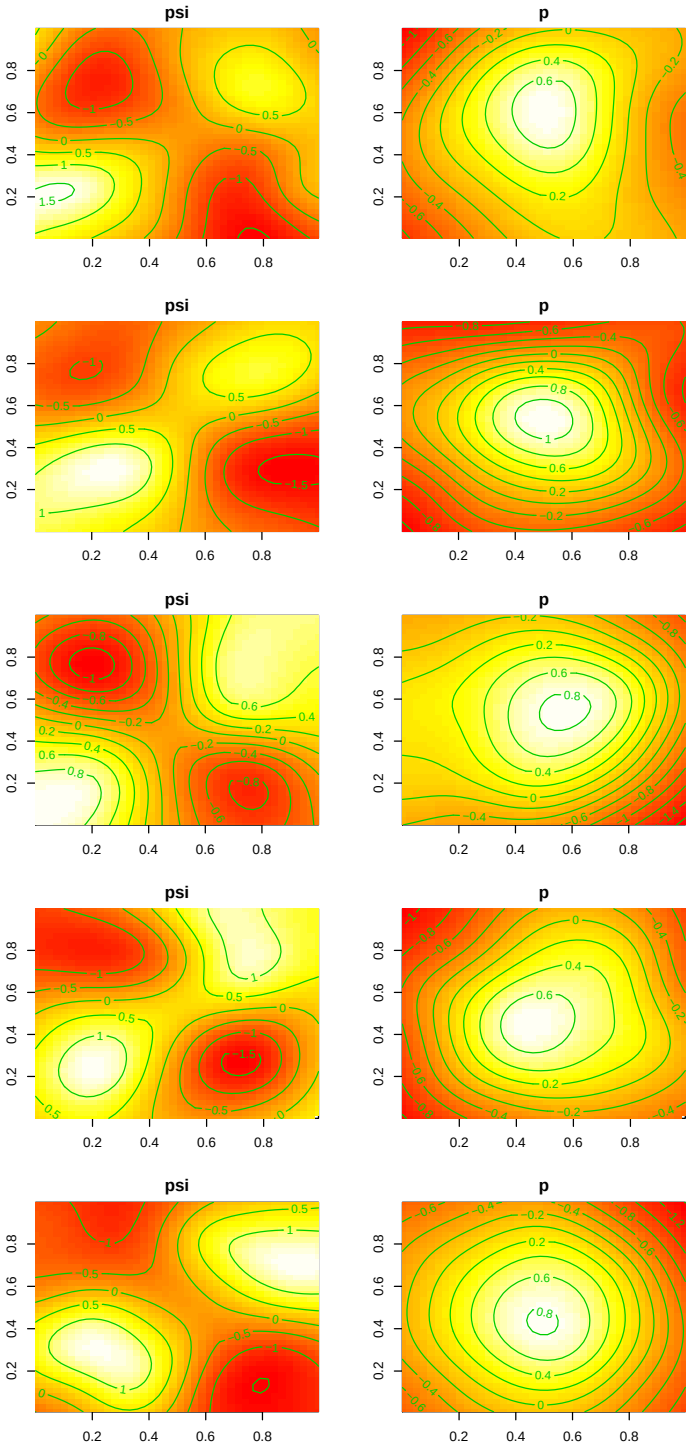


Figure 4: Fitted spatial smooths from the GAM model when the predictors in the two components of the model are disjoint. Each row of the figure corresponds to a separate simulation.

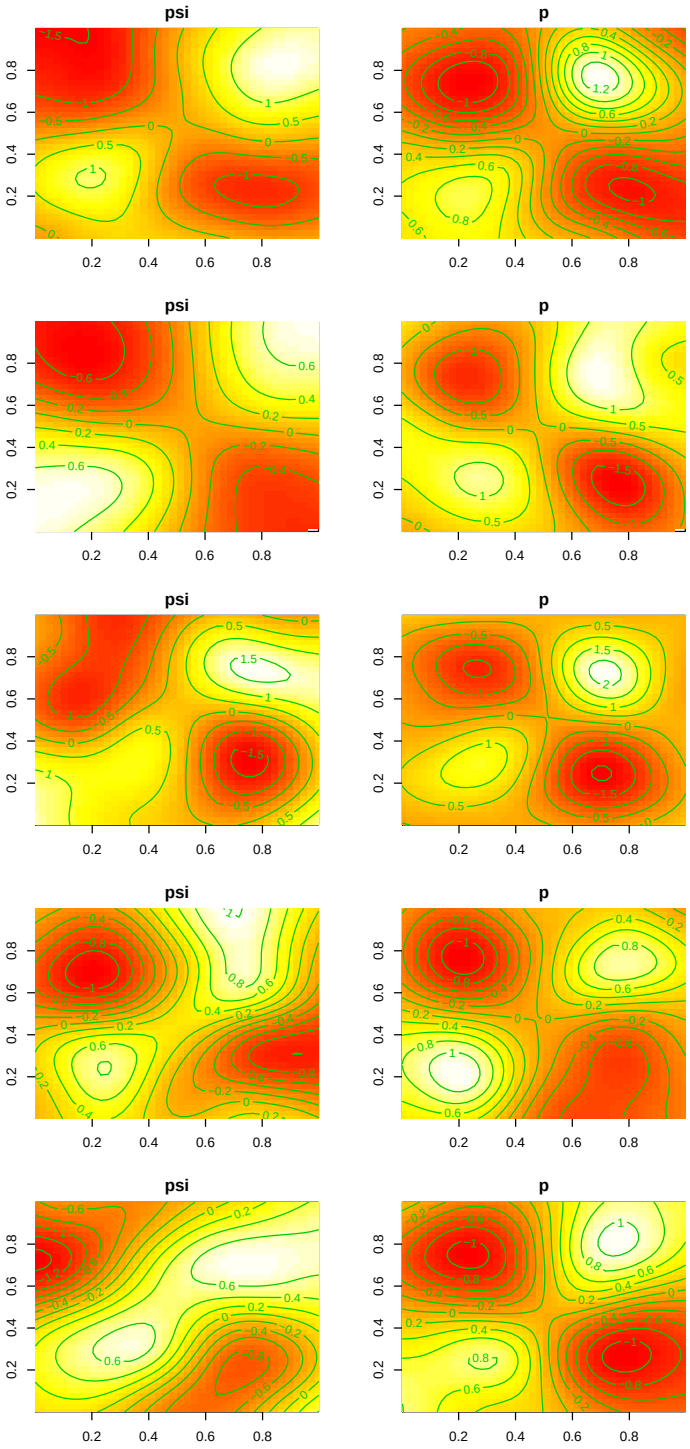


Figure 5: Fitted spatial smooths from the GAM model when the predictors in the two components of the model are not disjoint. Each row of the figure corresponds to a separate simulation.

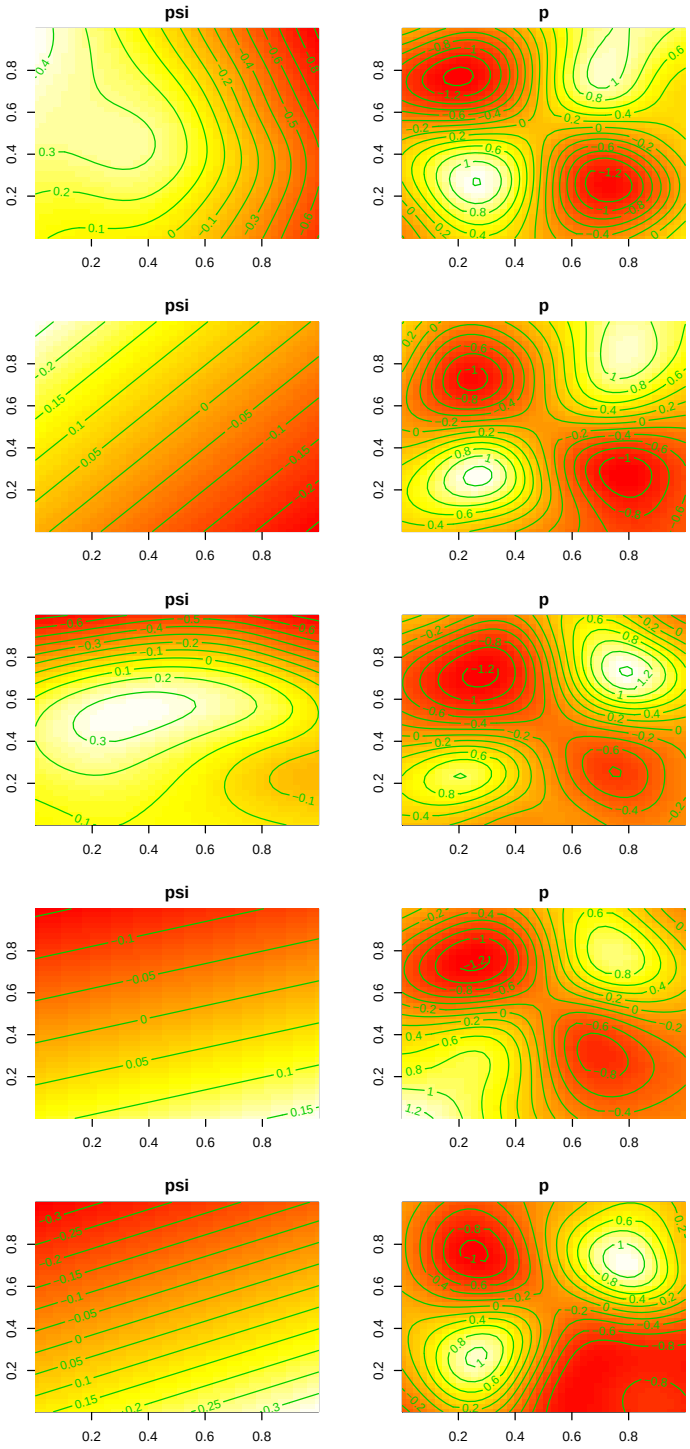


Figure 6: Fitted spatial smooths from the GAM model when only the p component of the model has spatial structure. Each row of the figure corresponds to a separate simulation.

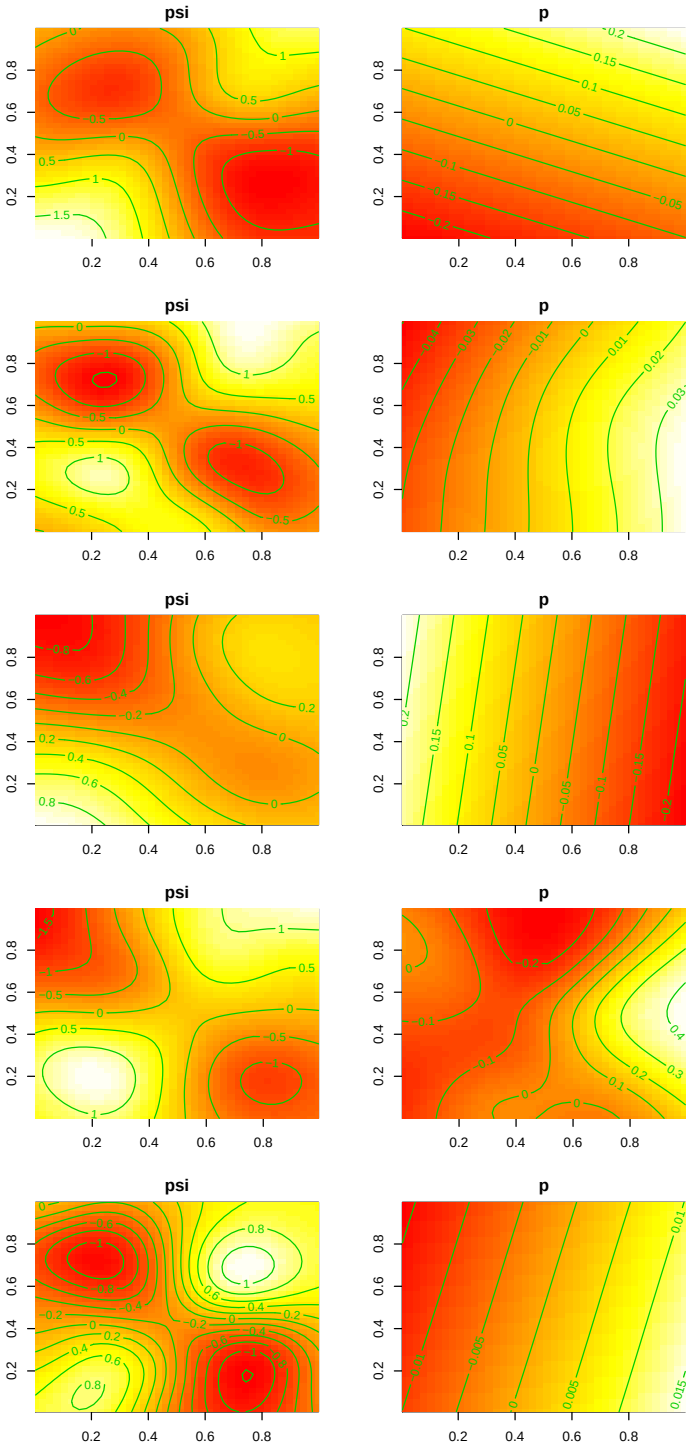


Figure 7: Fitted spatial smooths from the GAM model when only the ψ component of the model has spatial structure. Each row of the figure corresponds to a separate simulation.

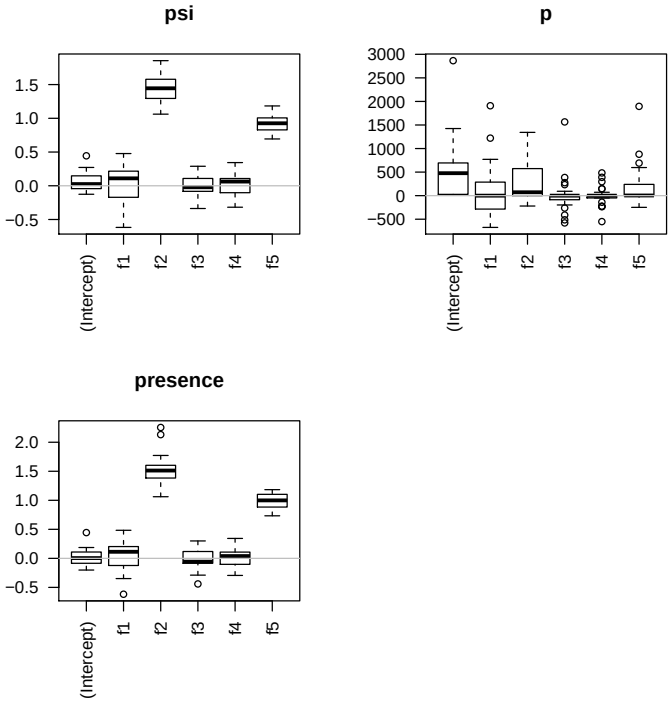


Figure 8: Boxplots of the fitted coefficients of the models when detection is perfect. The upper panels show the two components of zero inflated model, while the lower panel shows the coefficients of the presence-absence model.

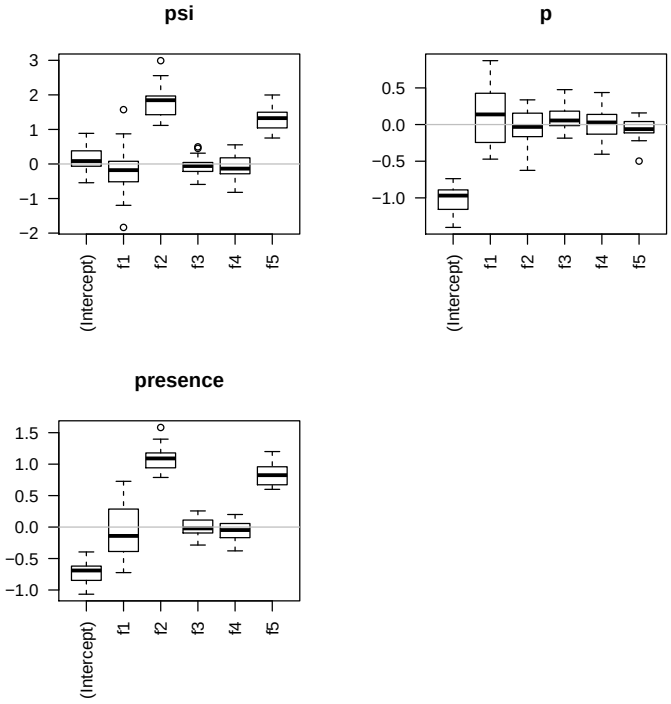


Figure 9: Boxplots of the fitted coefficients of the models when detection is poor. The upper panels show the two components of the zero inflated model, while the lower panel shows the coefficients of the presence-absence model.

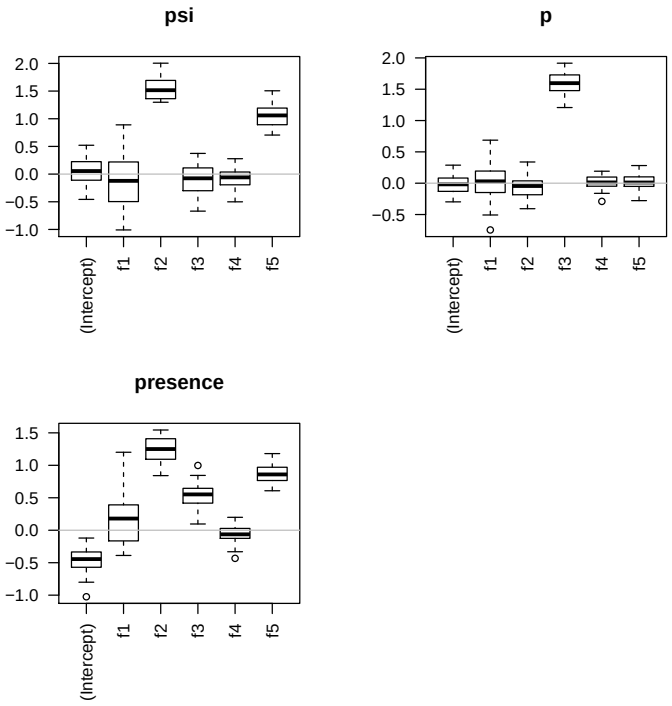


Figure 10: Boxplots of the fitted coefficients when detectability varies across the domain.

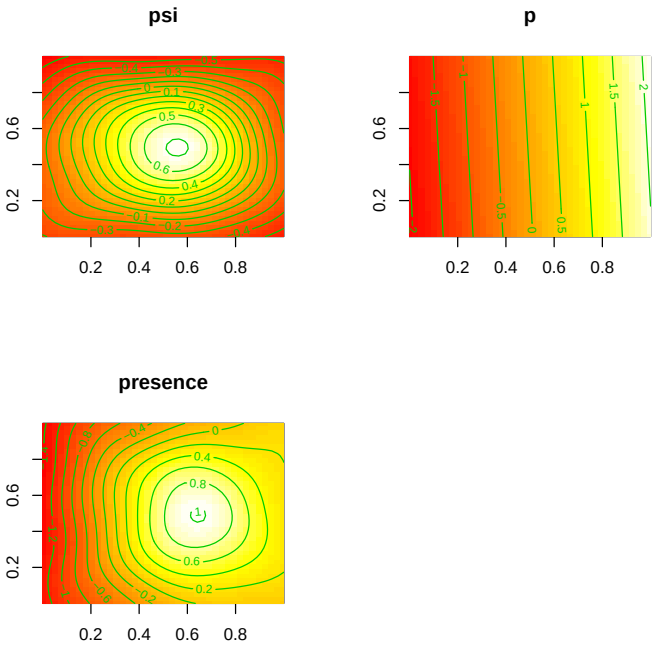


Figure 11: Fitted smooths from the GAM models when detectability varies across the domain.

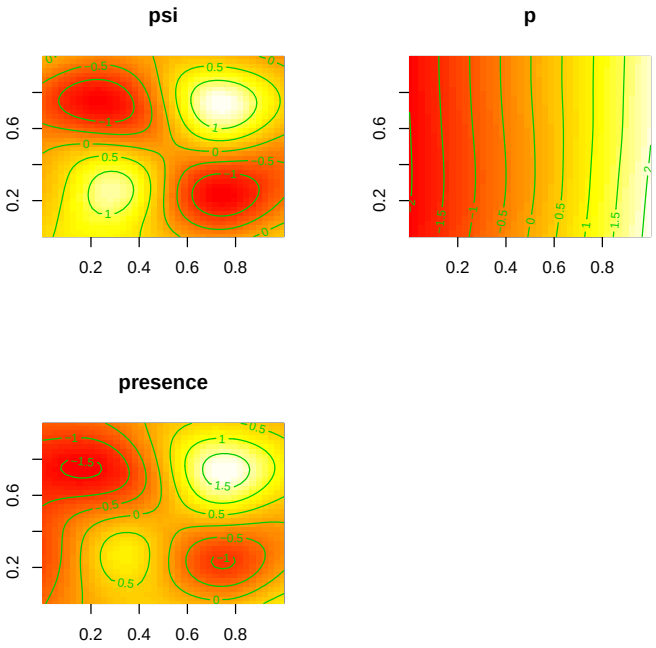


Figure 12: Fitted smooths from the GAM models when detectability varies across the domain.

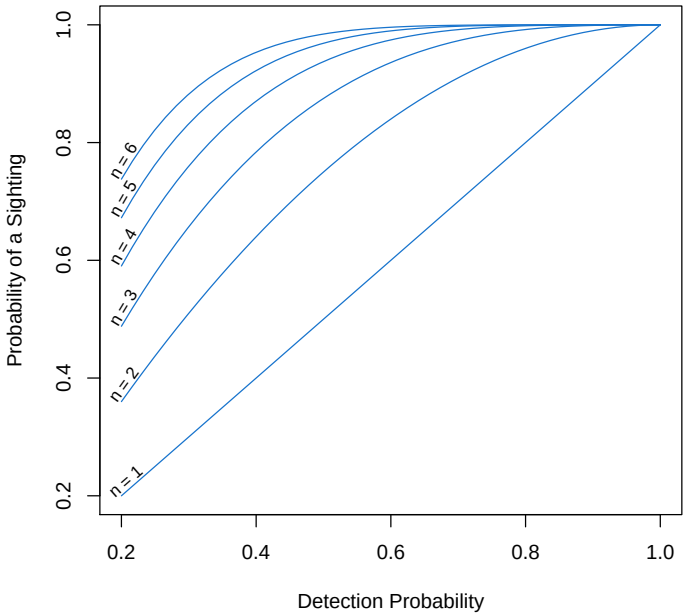


Figure 13: Probability of one or more sightings from n visits as a function of detection probability.

Appendix D R Implementation

This appendix presents functions in the R statistical language to fit, and simulate data from, zero-inflated occupancy models.

zib.em

The function `zib.em` fits a zero-inflated Binomial model by the EM algorithm. The EM algorithm alternately fits the detectability and occupancy components of the model until the fit converges. The user must specify formulae describing the two components of the model, and whether either of the two model components are to be fitted as a generalized additive model (GAM). In addition, the user can supply starting values for `p` and `psi`, the probabilities of detectability and occupancy, the minimum and maximum number of EM iterations to perform, and the tolerance on convergence.

```
> library(mgcv)
> ## Fit zero-inflated binomial models by EM.
> zib.em <- function(p.formula,psi.formula,data,
                     p=0.5,psi=0.5,p.gam=F,psi.gam=F,
                     min.em=10,max.em=500,tol=1.0E-6) {

   ## Log density
   dzib.log <- function(x,n,psi,p) {
     log(ifelse(x==0,(1-psi),0)+psi*dbinom(x,n,p))
   }


   ## Extract the response y
   mf <- model.frame(update(p.formula,.~1),data=data)
   Y <- model.response(mf)
   y <- Y[,1]
   n <- rowSums(Y)
   N <- length(y)

   ## Response for p component is the weights
   psi.formula <- update(psi.formula, w ~ .)
   environment(psi.formula) <- environment()
   environment(p.formula) <- environment()
   logLs <- double(max.em)
   for(k in 1:max.em) {
     ## Evaluate weights for current iteration
     w <- ifelse(y==0,psi*(1-p)^n/(1-psi+psi*(1-p)^n),1)
     ## Update models for current iteration
     fit.p <- if(p.gam)
       gam(p.formula,weights=w,family=binomial(),data=data)
     else
       glm(p.formula,weights=w,family=binomial(),data=data)
     fit.psi <- if(psi.gam)
       suppressWarnings(gam(psi.formula,family=binomial(),data=data))
     else
       suppressWarnings(glm(psi.formula,family=binomial(),data=data))
     ## Predict new psi, p
     psi <- predict(fit.psi,type="response")
     p <- predict(fit.p,type="response")
     ## Evaluate observed data likelihood
     logLs[k] <- sum(dzib.log(y,n,psi,p))
     if(k>min.em && abs(logLs[k]-logLs[k-1]) < tol) {
       logLs <- logLs[1:k]
       break
     }
   }
   ## Return results
   logL <- logLs[length(logLs)]
   df <- attr(logLik(fit.p),"df")+attr(logLik(fit.psi),"df")
   aic <- 2*(df-logL)
   fit <- list(fit.p=fit.p,fit.psi=fit.psi,
               p=p,psi=psi,w=w,logLs=logLs,
```

```
            logL=logL,aic=aic)
  class(fit) <- "zib"
  fit
}
```

This function returns an object consisting of the fits corresponding to the two components of the model. But as the model is fitted by EM, the standard errors and hypothesis tests from these two components are meaningless.

predict.zib

The predict method `predict.zib` for `zib` objects predicts either the probability of occupancy or detectability

```
> predict.zib <- function(object,type=c("occupancy","detectability"),...) {
   type <- match.arg(type)
   switch(type,
          occupancy=predict(object$fit.p,type="response",...),
          detectability=predict(object$fit.psi,type="response",...))
}
```

zib.sim

The function `zib.sim` allows data to be simulated from a known model. Data are simulated by first generating N random sites uniformly distributed on the $[0,1]\times[0,1]$ square. Predictors are calculated for each site and used to construct the probability ψ of occupancy at a site, and the probability p of detecting the animal if the site is occupied. At least one survey is conducted at every site, and the number of additional surveys is assumed Poisson.

```
> zib.sim <- function(N,predictors,p.coef,psi.coef,lambda=3) {
   ## Inverse logit transformation
   ilogit <- function(t) 1/(1+exp(-t))

   ## Spatial coordinates
   x <- runif(N)
   y <- runif(N)
   ## Predictors
   pr <- as.matrix(as.data.frame(lapply(predictors,function(f) f(x,y))))
   ## Probability of detection and occupancy
   p <- ilogit(cbind(1,pr)%*%p.coef)
   psi <- ilogit(cbind(1,pr)%*%psi.coef)
   ## Number of surveys at each site
   surveyed <- 1+rpois(N,lambda)
   ## Occupancy
   occupied <- rbinom(N,1,psi)
   ## Number sightings
   sighted <- occupied*rbinom(N,surveyed,p)
   cbind(data.frame(sighted=sighted,
                    surveyed=surveyed,
                    occupied=occupied,
                    p=p,psi=psi,x=x,y=y),
         as.data.frame(pr))
}
```

References

R Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Table A1

Form of models fitted and summary data including coefficients with standard errors, odds ratios and AIC values where Ψ =probability of occurrence, p = probability of detection and bracketed terms represent the covariates included in the models. *flower* = score 1-4; s(*lat*,*lon*) = bivariate smooth location term. Note that the AICs of the simple models and the AICs of the zero-inflated Binomial models (ZIBs) are not directly comparable. Likewise the AICs of PRESENCE models are not directly comparable to other models. Method indicates how the models were implemented, SAM – Spatial Analysis in Macro Ecology (Rangel et al. 2010), see R-vignettes for R packages and Appendix B and D for theory and implantation of EM Algorithm. Note that VGAM models absence rather than presence. To allow direct comparisons with other models and compute odds ratios the coefficients reported by VGAM have been negated. No standard errors are reported for the EM Algorithm coefficients as they are not considered reliable (see Appendix B). The best models for p=1 are shaded orange and best ZIBs are shaded blue. a) 2009, b) 2010, c) 2011, d) 2012

Table A1 a) 2009

Model	Method	Response	*flower* coeff (se)	*flower* odds ratio	Intercept (se)	AIC
Ψ(*flower*) .p(1)	SAM - logistic	Ψ	1.4 (0.13)	4.05	-3.8 (0.26)	288
Ψ(*flower+cW*) .p(1)	SAM -Auto-logistic	Ψ	1.2 (0.14)	3.32	-5.2 (0.40)	251
Ψ(*flower+s(lat,lon)*) .p(1)	mgcv	Ψ	1.6 (0.22)	4.95	-10.3 (3.2)	236.5
Ψ(*flower*).p(*flower*)	PRESENCE	Ψ	1.01 (0.24)	2.75	-1.98 (0.60)	654
		p	0.90 (0.18)	2.5	-2.60 (0.55)	
Ψ(*flower*).p(*flower*)	R - VGAM	Ψ	0.95 (0.11)	2.6	1.8 (0.13)	448[#]
		p	0.94 (0.10)	2.6	-2.7 (0.26)	
Ψ(*flower*).p(*flower*)	R- EM Algorithm	Ψ	1.01	2.75	-1.98	448
		p	0.90	2.5	-2.60	
Ψ(*flower*).p(*flower* + *s*(*lat,lon*))	R - EM Algorithm	Ψ	0.40	1.5	0.77	400
		p	1.44	4.2	-6.72	
Ψ(*flower* + *s(lat,lon)*)).p(*flower*)	R - EM Algorithm	Ψ	0.97	2.64	-2.2	440
		p	0.88	2.41	-2.5	
Ψ(*flower* + *s(lat,lon)*).p(*flower+s(lat,lon)*)	R - EM Algorithm	Ψ	0.65	1.91	-0.2	390
		p	1.4	4.05	-7.78	

convergence not obtained after 30 iterations

Table A1 b) 2010

Model	Method	Response	*flower* coeff (se)	*flower* odds ratio	Intercept (se)	AIC
Ψ(*flower*) .p(1)	SAM - logistic	Ψ	0.5 (0.07)	1.65	-2.23 (0.15)	756
Ψ(*flower+cW*) .p(1)	SAM -Auto-logistic	Ψ	0.5 (0.09)	1.65	-4.99 (0.32)	509
Ψ(*flower+s(lat,lon)*) .p(1)	R - mgcv	Ψ	0.47 (0.10)	1.60	-3.66 (0.64)	507
Ψ(*flower*).p(*flower*)	PRESENCE	Ψ	0.56 (0.10)	1.75	-1.86 (0.21)	1305
		p	0.08 (0.11)	1.08	-0.41 (0.26)	
Ψ(*flower*).p(*flower*)	R - VGAM	Ψ	0.56 (0.08)	1.75	1.86 (0.17)	1035
		p	0.08 (0.09)	1.08	-0.41 (0.23)	
Ψ(*flower*).p(*flower*)	R- EM Algorithm	Ψ	0.57	1.77	-1.86	1035
		p	0.08	1.08	-0.41	
Ψ(*flower*).p(*flower* + *s*(*lat,lon*))	R - EM Algorithm	Ψ	0.43	1.54	0.94	807
		p	0.34	1.40	-4.25	
Ψ(*flower* + *s(lat,lon)*)).p(*flower*)	R - EM Algorithm	Ψ	0.43	1.53	-3.2	808
		p	0.13	1.14	-0.36	
Ψ(*flower* + *s(lat,lon)*).p(*flower+s(lat,lon)*)	R - EM Algorithm	Ψ	0.67	1.95	2.9	783
		p	0.32	1.37	-4.2	

Table A1 c) 2011

Model	Method	Response	*flower* coeff (se)	*flower* odds ratio	Intercept (se)	AIC
Ψ(*flower*) .p(1)	SAM - logistic	Ψ	1.1 (0.09)	3.0	-2.9 (0.15)	571
Ψ(*flower+cW*) .p(1)	SAM -Auto-logistic	Ψ	0.9 (0.10)	2.46	-5 (0.30)	458
Ψ(*flower+s(lat,lon)*) .p(1)	R - mgcv	Ψ	1.1 (0.13)	3.0	-5.1 (0.62)	447
Ψ(*flower*).p(*flower*)	PRESENCE	Ψ	1.15 (0.16)	3.16	-2.2 (0.24)	1006
		p	0.35 (0.09)	1.42	-1.15(0.26)	
Ψ(*flower*).p(*flower*)	R - VGAM	Ψ	1.15 (0.12)	3.16	2.24(0.14)	782
		p	0.35 (0.08)	1.42	-1.11 (0.20)	
Ψ(*flower*).p(*flower*)	R- EM Algorithm	Ψ	1.15	3.16	-2.24	782
		p	0.35	1.42	-1.11	
Ψ(*flower*).p(*flower* + *s*(*lat,lon*))	R - EM Algorithm	Ψ	1.77	5.87	-0.87	672
		p	0.40	1.49	-4.6	
Ψ(*flower* + *s(lat,lon)*)).p(*flower*)	R - EM Algorithm	Ψ	1.9	6.69	-5.58	665
		p	0.27	1.31	-0.99	
Ψ(*flower* + *s(lat,lon)*).p(*flower+s(lat,lon)*)	R - EM Algorithm	Ψ	1.97	7.17	-1.0	671
		p	0.36	1.43	-4.63	

Table A1 d) 2012

Model	Method	Response	*flower* coeff (se)	*flower* odds ratio	Intercept (se)	AIC
Ψ(*flower*) .p(1)	SAM - logistic	Ψ	1.07 (0.08)	2.92	-3.022	631.5
Ψ(*flower+cW*) .p(1)	SAM -Auto-logistic	Ψ	0.85	2.34	-5.102	488
Ψ(*flower+s(lat,lon)*) .p(1)	R - mgcv	Ψ	1.04 (0.11)	2.83	-3.8 (0.28)	472.9
Ψ(*flower*).p(*flower*)	PRESENCE	Ψ	0.80 (0.14)	2.23	-1.84 (0.36)	1003
		p	0.67 (0.13)	1.95	-1.5 (0.38)	
Ψ(*flower*).p(*flower*)	R - VGAM	Ψ	0.78	2.18	1.77	832
		p	0.70	2.01	-1.61	
Ψ(*flower*).p(*flower*)	R- EM Algorithm	Ψ	0.78	2.18	1.81	832
		p	0.69	1.99	-1.59	
Ψ(*flower*).p(*flower* + *s*(*lat,lon*))	R - EM Algorithm	Ψ	1.22	3.38	0.60	683
		p	0.8	2.23	14.6	
Ψ(*flower* + *s(lat,lon)*)).p(*flower*)	R - EM Algorithm	Ψ	0.69	1.99	-2.54	694
		p	0.66	1.93	-1.28	
Ψ(*flower* + *s(lat,lon)*).p(*flower+s(lat,lon)*)	R - EM Algorithm	Ψ	0.90	2.46	2.07	686
		p	0.87	2.39	-23.1	

Figure A2

Spatial autocorrelation in residuals of simple binomial models with (green diamonds) and without a smooth location covariate (black circles) for each year of the study. Shaded areas represent values that are not significantly spatially autocorrelated as indicated by Morans I test.

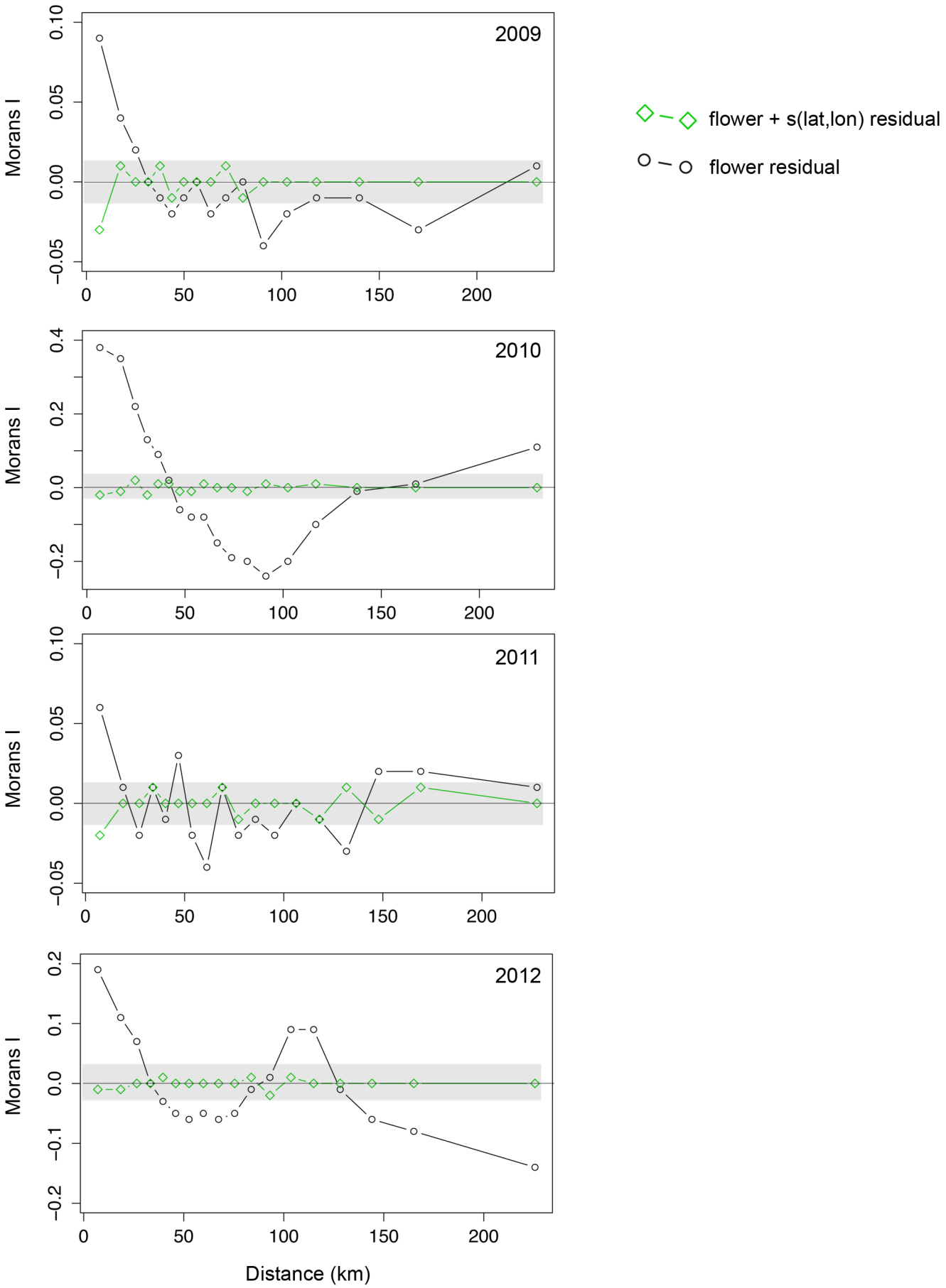


Figure A3

Range of detection probabilities predicted from models with a) no spatial covariate in the zero-inflated model Ψ(flower).p(flower) and b) spatial covariate in the detection component of the model Ψ(flower).p(flower + s(lat,lon))

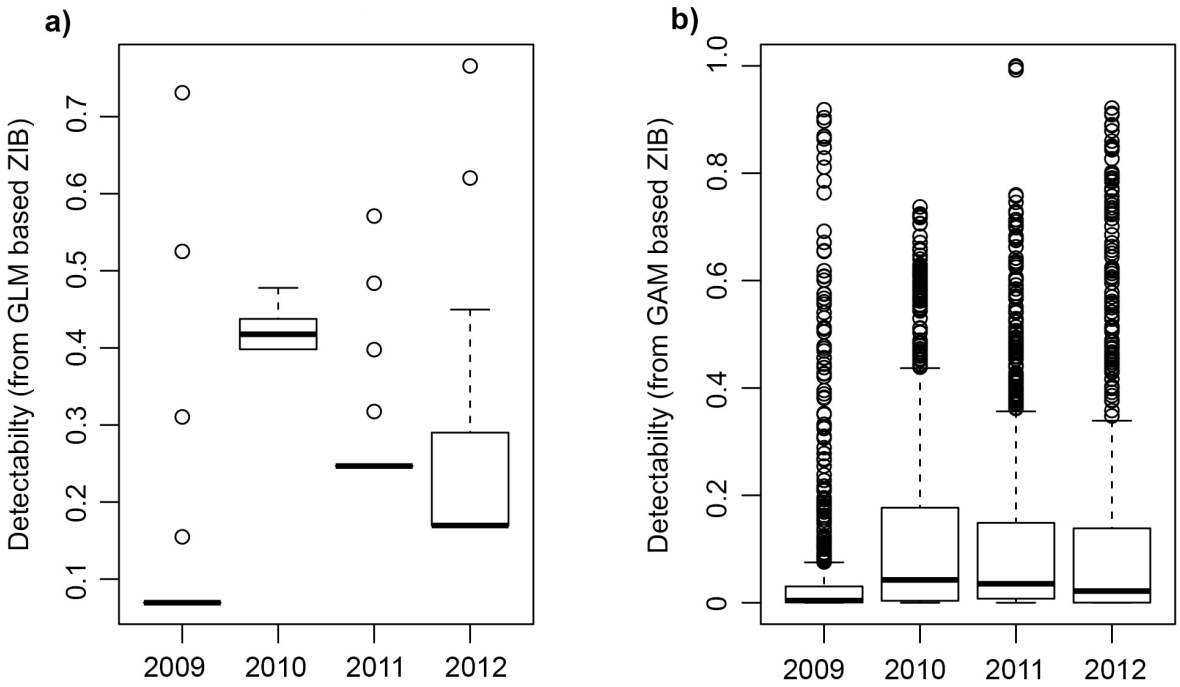


Figure A4

a) Detectability predictions from the zero-inflated Binomial models (ZIB) with spatial covariate in the detectability component Ψ(flower).p(flower + s(lat,lon)), b) detectabilty predictions from the ZIB with no spatial covariate Ψ(flower).p(flower) and c) occupancy predictions from the ZIB with spatial covariate in the detectability component

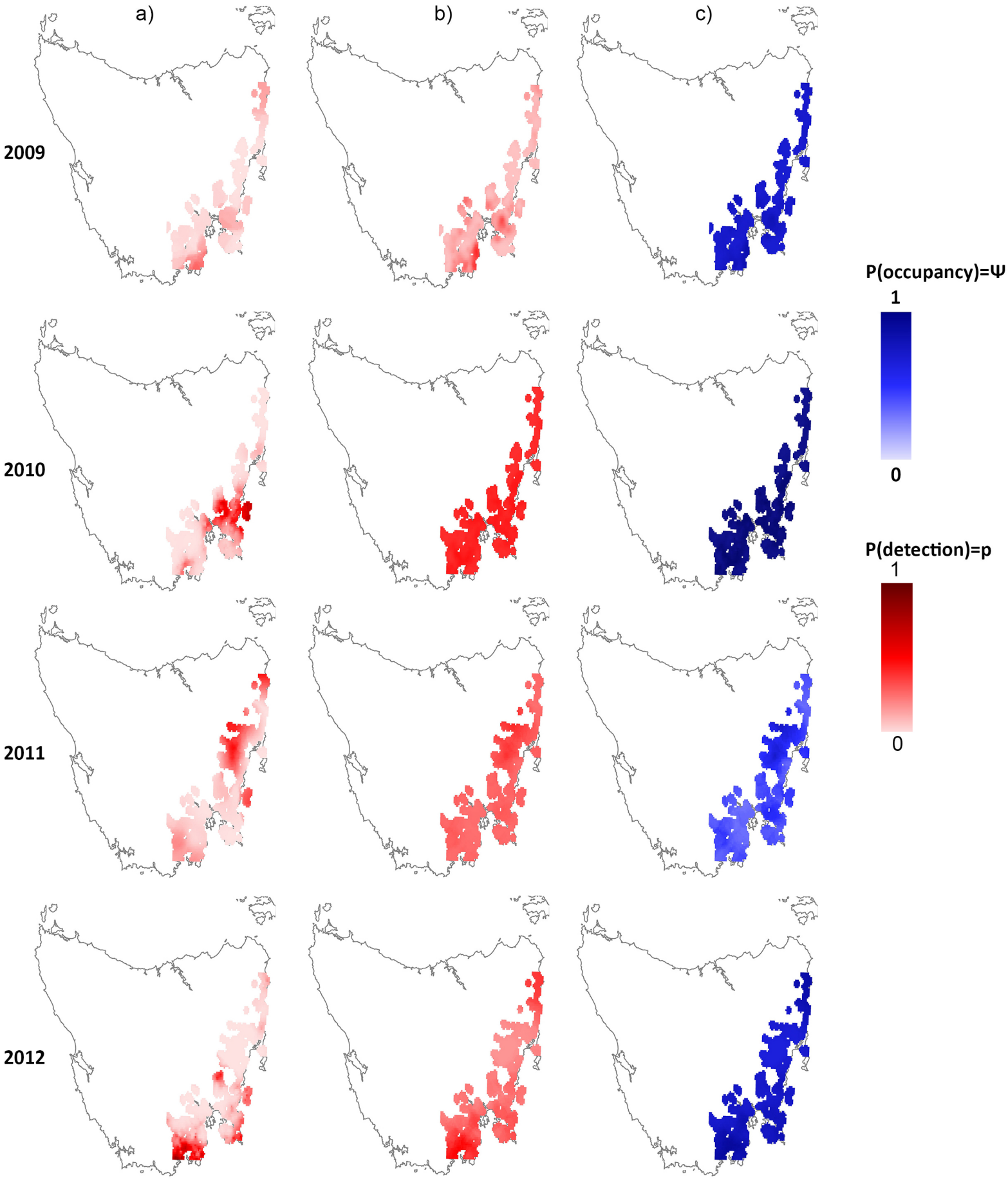


Figure A5

a) Occupancy and b) detectability predictions from the zero-inflated Binomial models (ZIB) with spatial covariate in both the occupancy and detectability component Ψ(flower + s(lat,lon)).p(flower + s(lat,lon))

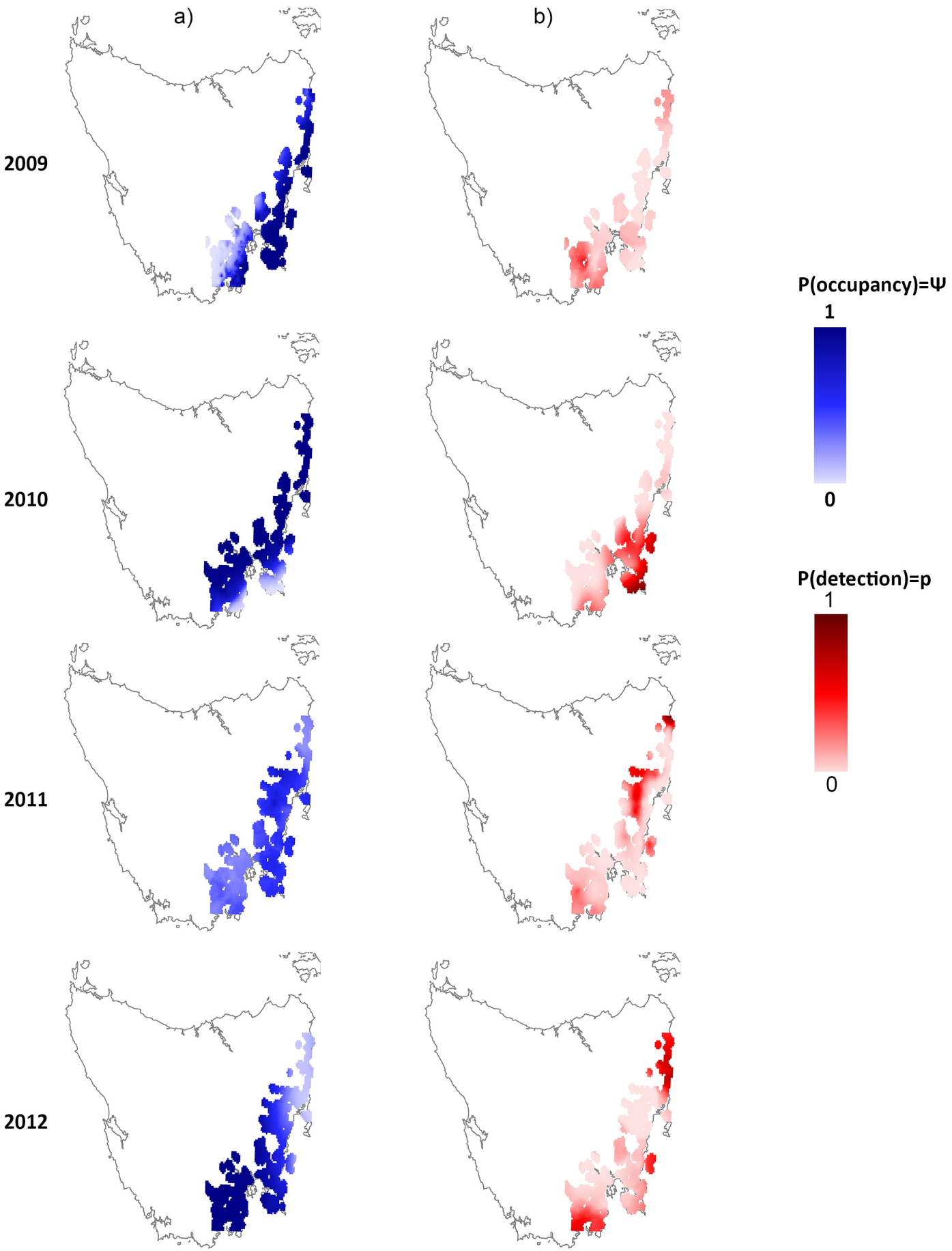


Figure A6

Range of occupancy probabilities predicted from models with a) no spatial covariate in the zero-inflated model Ψ(flower).p(flower) and b) spatial covariate in the occupancy component of the model Ψ(flower+ s(lat,lon).p(flower)

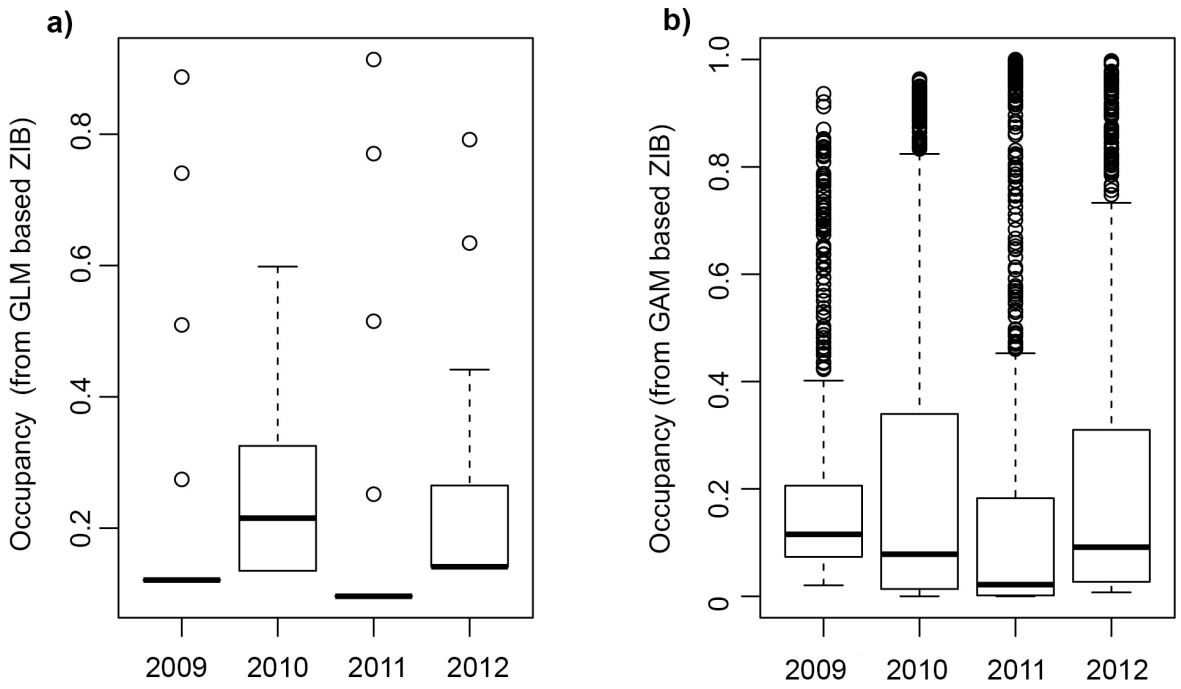


Figure A7

Comparisons of occupancy predictions from simple binomial GAM models- Ψ(flower+s(lat,lon)) .p(1) and occupancy predictions from zero-inflated Binomial models (ZIB) with spatial covariate in the occupancy component only - Ψ(flower + s(lat,lon))).p(flower)

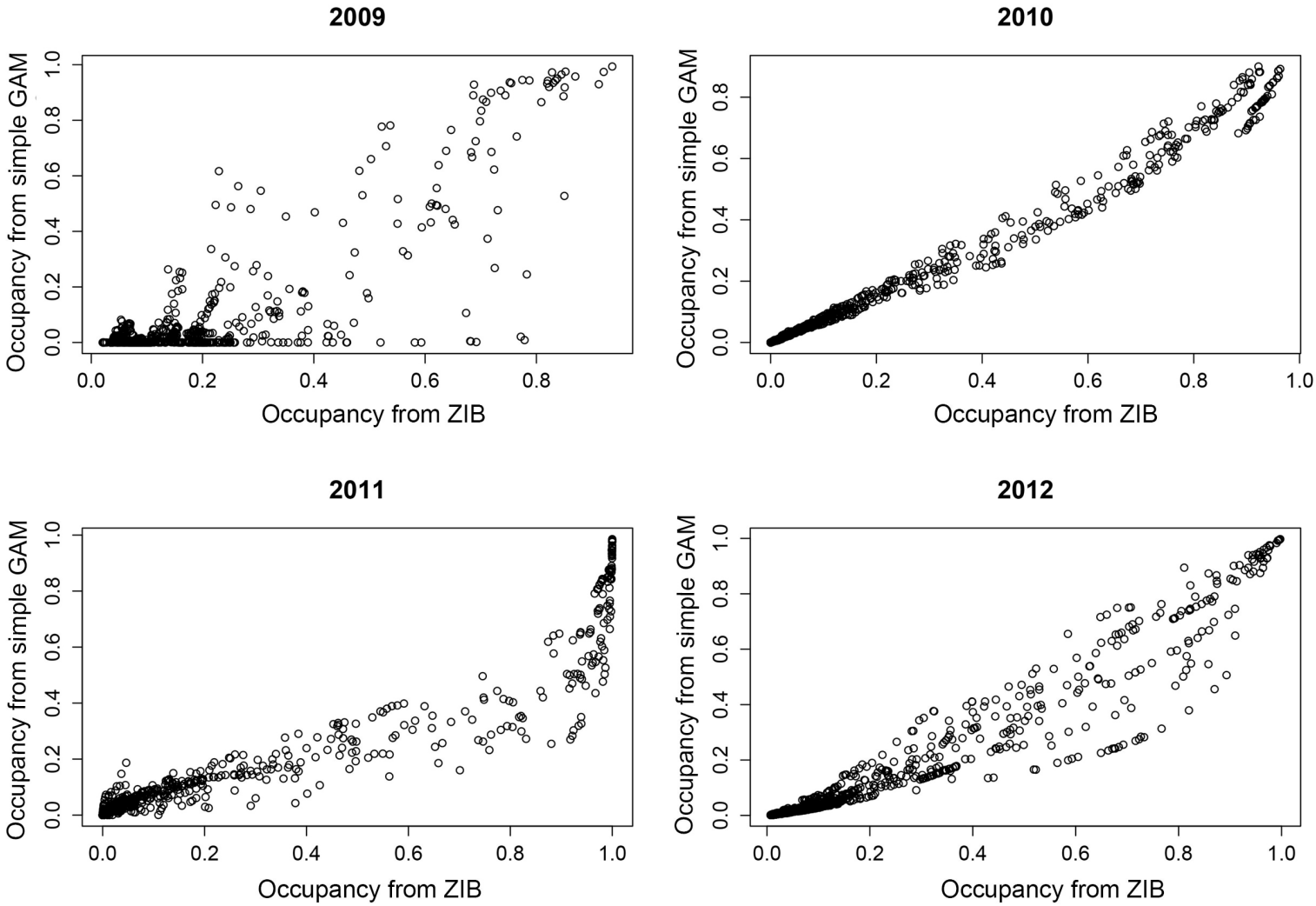
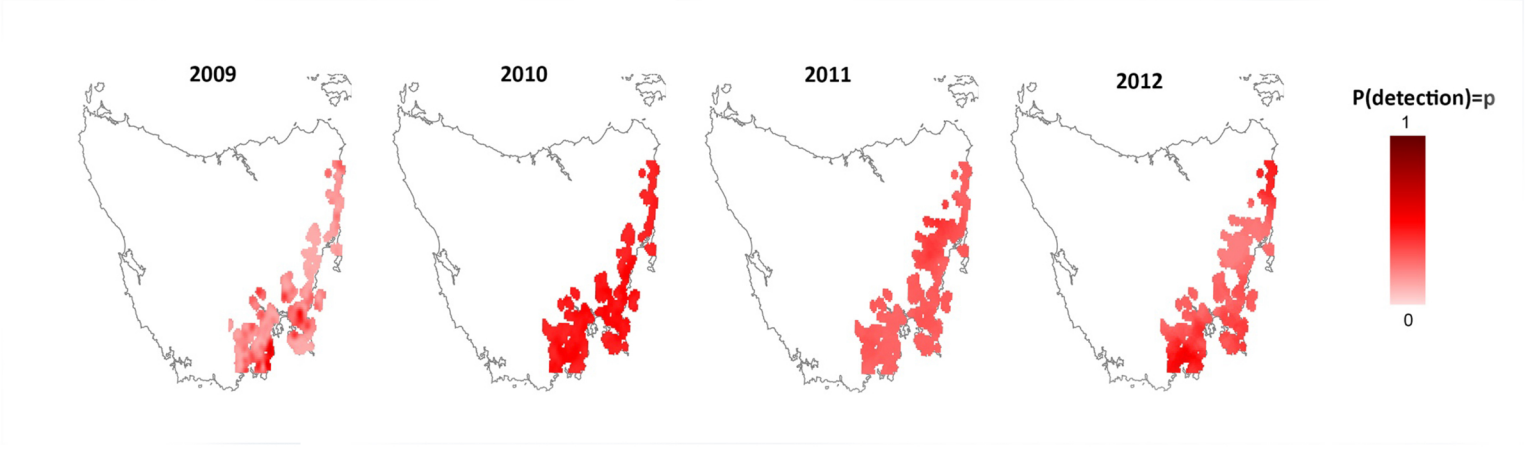


Figure A8

Prediction maps of swift parrot detectability for 2009-2012 using zero-inflated Binomial models with a spatial covariate in the occupancy component and no spatial covariate in the detectability component $\Psi(flower + s(lat,lon))).p(flower)$



Chapter 4 Appendix

Appendix S1. Supporting Map

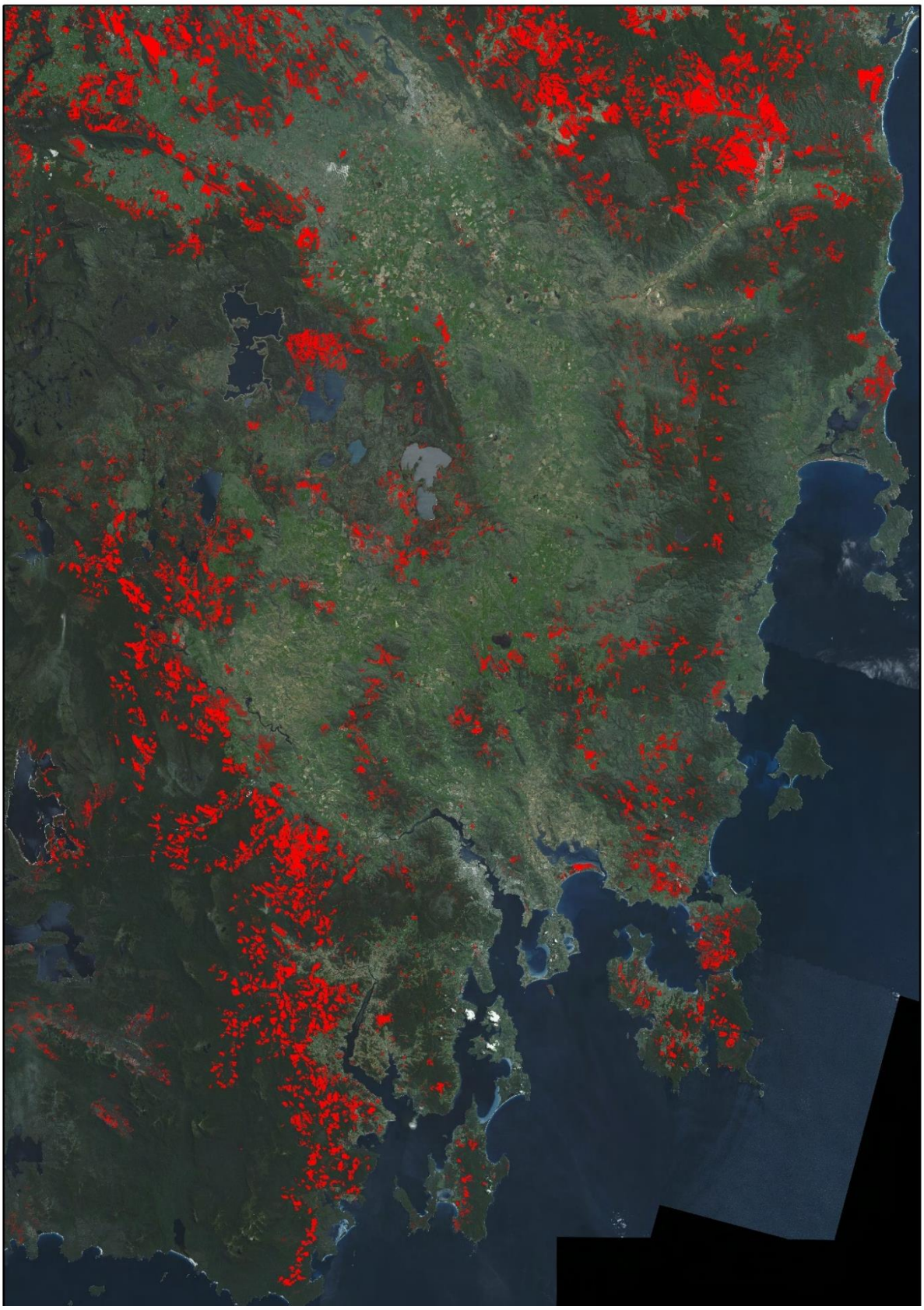


Figure S1. Forest loss/disturbance (red) in Tasmania from ~1997-2013 (adapted from Hansen et al. 2013). Dark green generally indicates forested areas, light green is generally non-forested environments.

Appendix S2. Supporting Figure

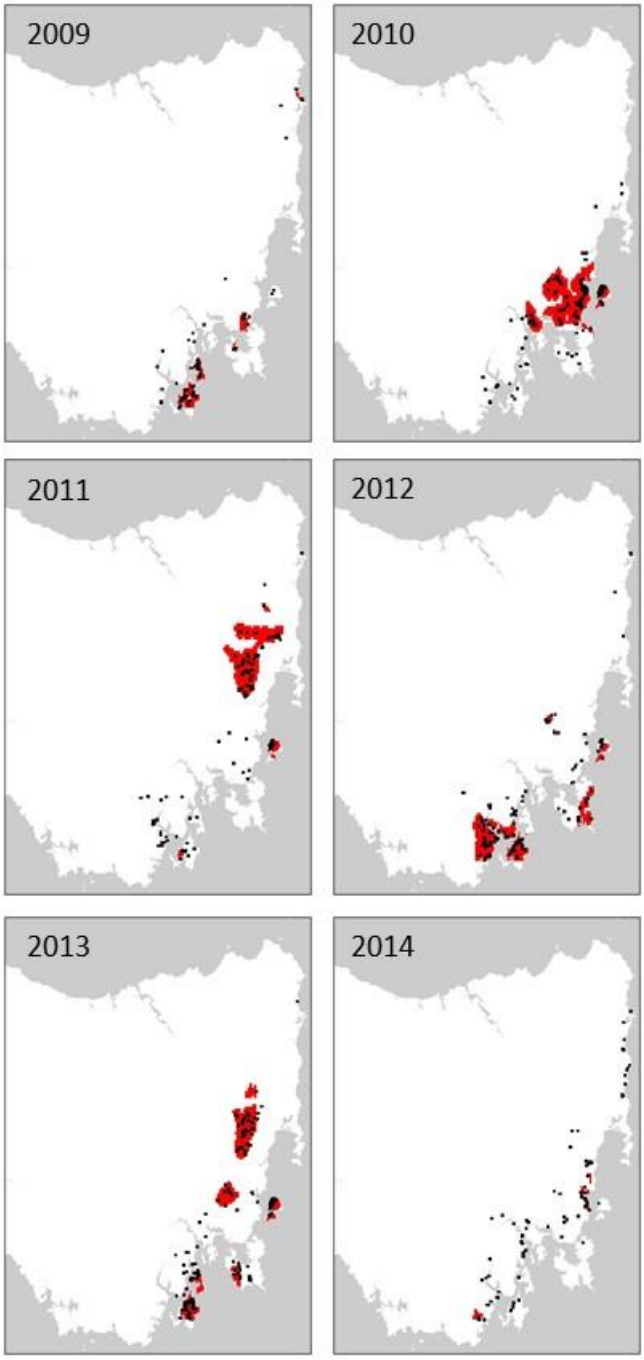


Figure S2. Swift parrot occupancy model predictions of TOTAL AREA from 2009-2014 showing sites where birds were detected (black squares, N=769).

Appendix S3. Supporting Tables

Table S1. Model summaries for annual swift parrot occupancy models implemented as per Webb et al. (2014); s(lat, long) = bivariate smoothed spatial term, flower = site-level flower score.

	s(lat, long)		Flower			
Year	χ^2	*p*	z-value	*p*	Adjusted R^2	Deviance
2009	174.7	<0.0001	21.1	<0.0001	0.56	56%
2010	296.6	<0.0001	5.6	<0.0001	0.62	61%
2011	313.3	<0.0001	23.0	<0.0001	0.62	62%
2012	499.3	<0.0001	12.7	<0.0001	0.64	64%
2013	340.4	<0.0001	13.2	<0.0001	0.59	62%
2014	68.3	<0.0001	20.4	<0.0001	0.41	43%

Table S2. Metrics of Maxent model performance and variable effect sizes. Eucalypt forest and woodland (EucFor), Maximum temperature (MaxTemp), Minimum temperature (MinTemp), Average maximum temperature (AvMaxTemp), Average minimum temperature (AvMinTemp), Average rainfall (AvRain), Total rainfall (TotRain). Temperature and rainfall variables are for the preceding 12 months. The similarity between training and test AUC statistics indicates model fit is good.

		AUC			Equal training sensitivity and specificity		Percent contribution (permutation importance)						
Year	Occurrences used	Training	Test	Prevalence	Training omission	Test omission	EucFor	MaxTemp	MinTemp	AvMaxTemp	AvMinTemp	AvRain	TotRain
2009	66	0.950	0.814	0.07	0.12	0.10	1.09	8.0	26.08	13.01	21.41	21.26	9.17
2010	143	0.971	0.911	0.04	0.07	0.05	0.21	15.22	14.58	0.20	18.56	46.63	1.86
2011	126	0.947	0.875	0.09	0.13	0.10	5.76	13.78	10.17	9.19	7.98	52.11	1.01
2012	142	0.967	0.888	0.05	0.11	0.12	0.01	33.90	16.30	7.68	7.78	33.81	0.52

Table S3. The number of sampled 1 km^2 grid cells in potential swift parrot nesting habitat over 6 years of monitoring, and the number of sampling locations per cell.

Year	Number of 1 km^2 cells sampled	Mean sampling visits per cell	Range of sampling visits
2009	51	8.5	3-39
2010	127	3.2	1-16
2011	127	2.7	1-10
2012	152	2.1	1-8
2013	189	2.5	1-9
2014	119	2.8	1-13

Table S4. Pearson product-moment correlations (r) comparing different metrics of occupied habitat within and between modeling approaches.

Correlation	Measure of habitat	Value		
Correlations comparing estimates between habitat suitability models and occupancy models	TOTAL AREA	$t = 0.68$	$p = 0.57$	$r = 0.43$
	FOREST	$t = 1.46$	$p = 0.28$	$r = 0.72$
	NESTING HABITAT	$t = 1.69$	$p = 0.23$	$r = 0.77$
	ADJUSTED NESTING HABITAT	$t = 1.35$	$p = 0.31$	$r = 0.69$
Correlations comparing FORAGING HABITAT estimates with other metrics from the occupancy models	TOTAL AREA versus FORAGING HABITAT	$t = 2.16$	$p = 0.1$	$r = 0.73$
	FOREST versus FORAGING HABITAT	$t = 1.29$	$p = 0.27$	$r = 0.54$
	NESTING versus FORAGING HABITAT	$t = 1.36$	$p = 0.25$	$r = 0.56$
	ADJUSTED NESTING HABITAT versus FORAGING HABITAT	$t = 1.41$	$p = 0.23$	$r = 0.58$

Table S5. Percentage of occupied sites captured by the habitat suitability models and occupancy models with their respective threshold applied.

	Year					
	2009	2010	2011	2012	2013	2014
Occupancy model	64%	77%	64%	60%	78%	18%
Habitat suitability model	94%	93%	87%	89%	-	-
Difference between modeling approaches	30%	16%	23%	29%	NA	NA

Table S6. Mean estimate of occupancy in cells falling outside the TOTAL AREA map identified by the occupancy models (2009-2012).

Year	**Mean occupancy**	**S.D.**
2009	0.161	0.083
2010	0.083	0.092
2011	0.099	0.106
2012	0.094	0.093

Table S7. Estimates of different types of occupied habitat based on habitat suitability models versus occupancy models.

		Year					
	Metric (km^2)	2009	2010	2011	2012	2013	2014
Habitat suitability models	TOTAL AREA	3515	3971	5911	3688	-	-
	FOREST	1856	2170	3936	2472	-	-
	FORAGING HABITAT	172	217	241	201	-	-
	NESTING HABITAT	1141	1538	2575	1604	-	-
	ADJUSTED NESTING HABITAT	379	548	967	600	-	-
Occupancy models	TOTAL AREA	377	1498	1084	1070	1286	131
	FOREST	212	845	963	687	974	62
	FORAGING HABITAT	23	98	20	40	49	7.5
	NESTING HABITAT	133	652	625	314	701	41
	ADJUSTED NESTING HABITAT	43	257	265	83	272	11
	TOTAL BAOO	66	355	285	123	321	19
TOTAL AREA overlap of habitat suitability models with occupancy models		327	1210	839	705	-	-

Appendix S4. Sensitivity Analyses

We conducted a sensitivity analysis to explore the effect of the threshold selected for assigning species presence versus absence to occupancy models on the location of areas occupied by the swift parrot each year. There was no evidence that differences between the modeling approaches was an artefact of their respective thresholds.

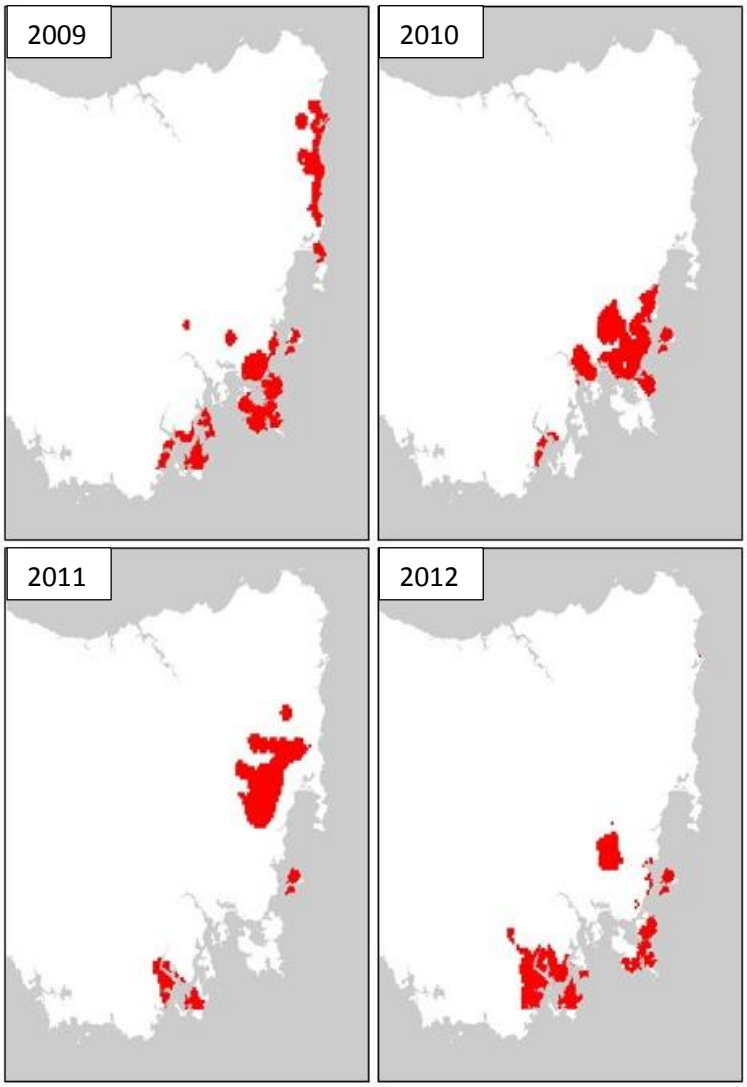


Figure S3. Swift Parrot occupancy models from 2009-2012 with half the mid-point threshold value applied. The increase in area captured as a result of lowering the threshold clearly follows a different pattern to the habitat suitability models (see main text Figure 1).

Chapter 5 Appendix

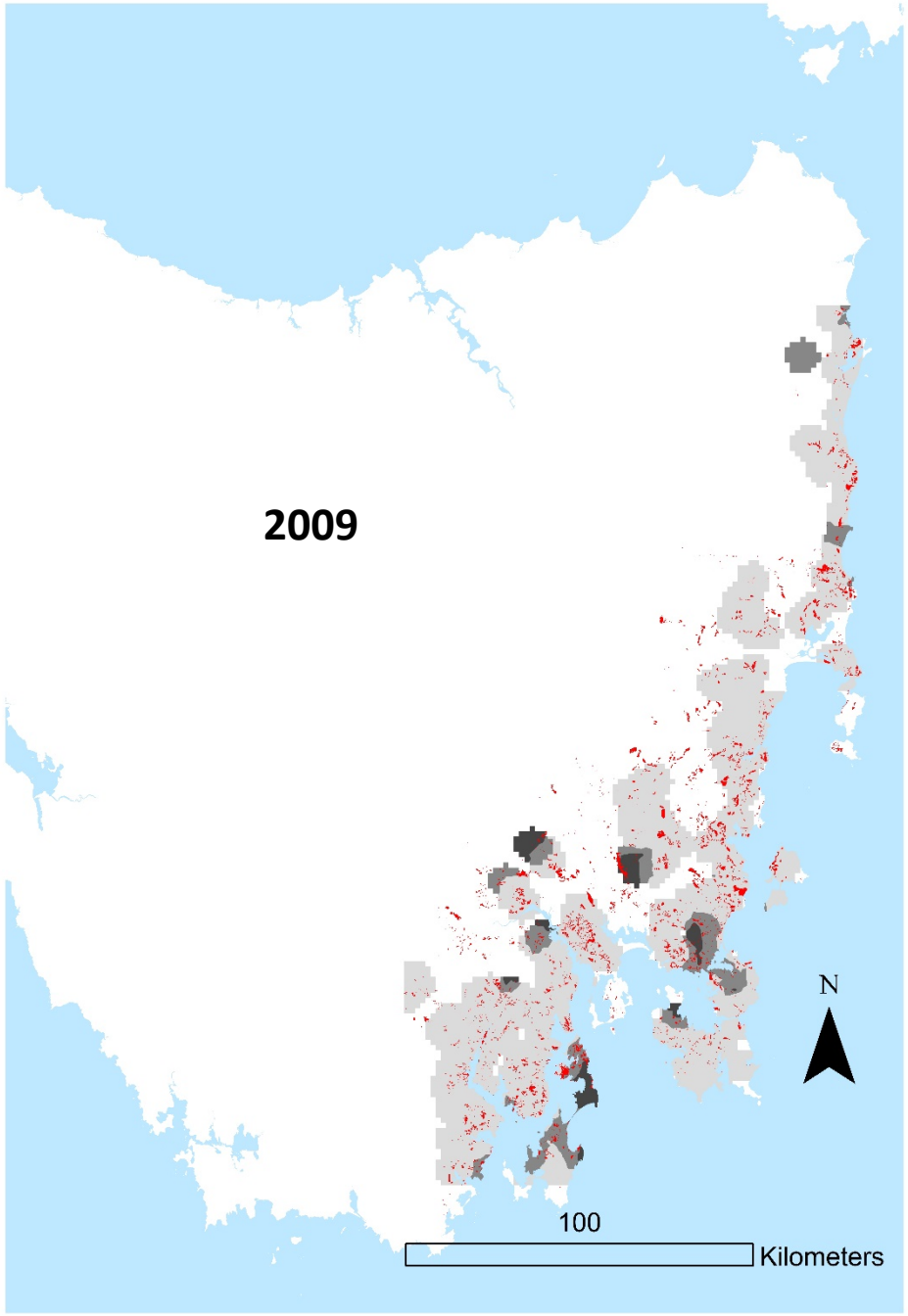
Appendix A

Figure S1a. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

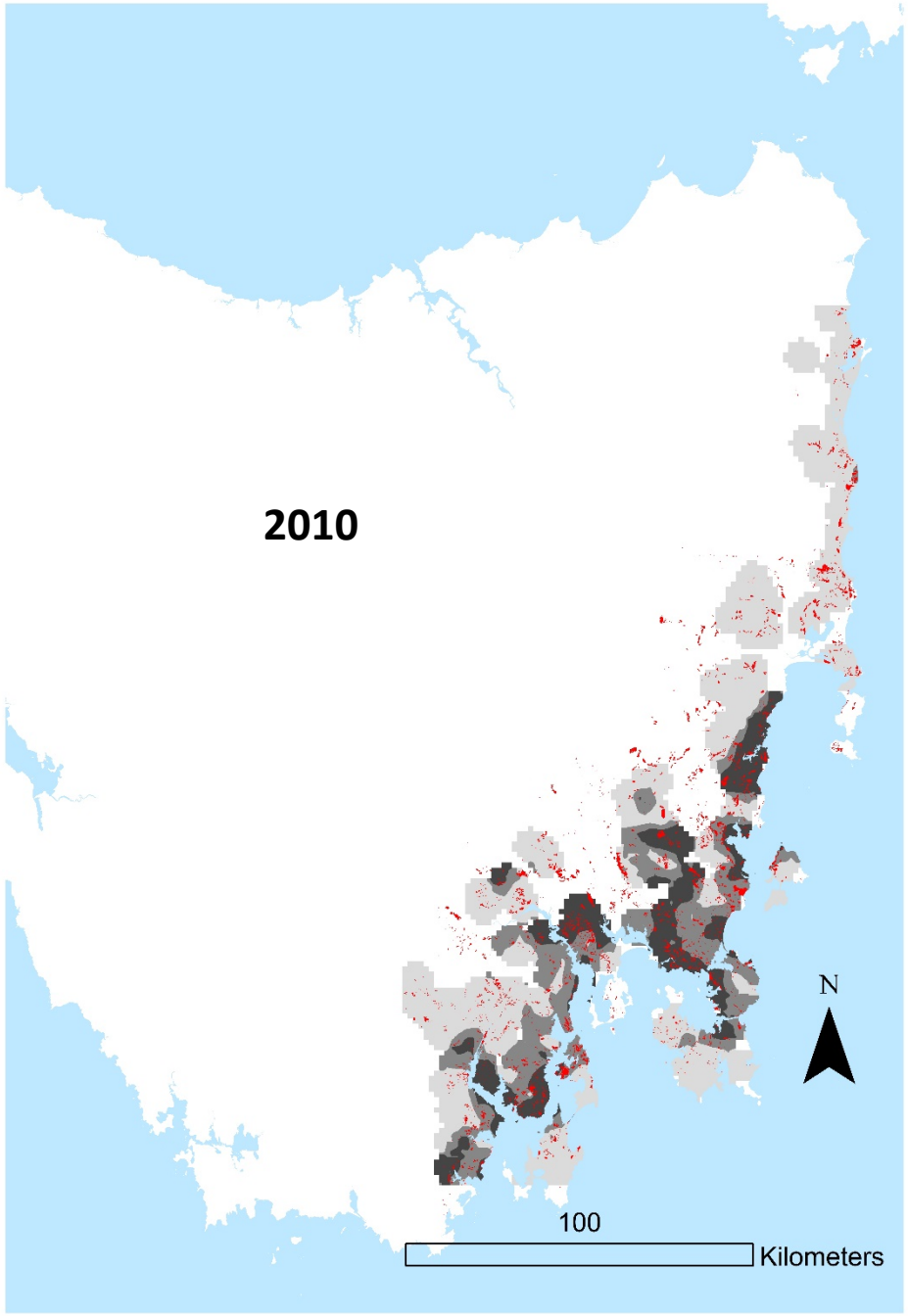
Appendix A

Figure S1b. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

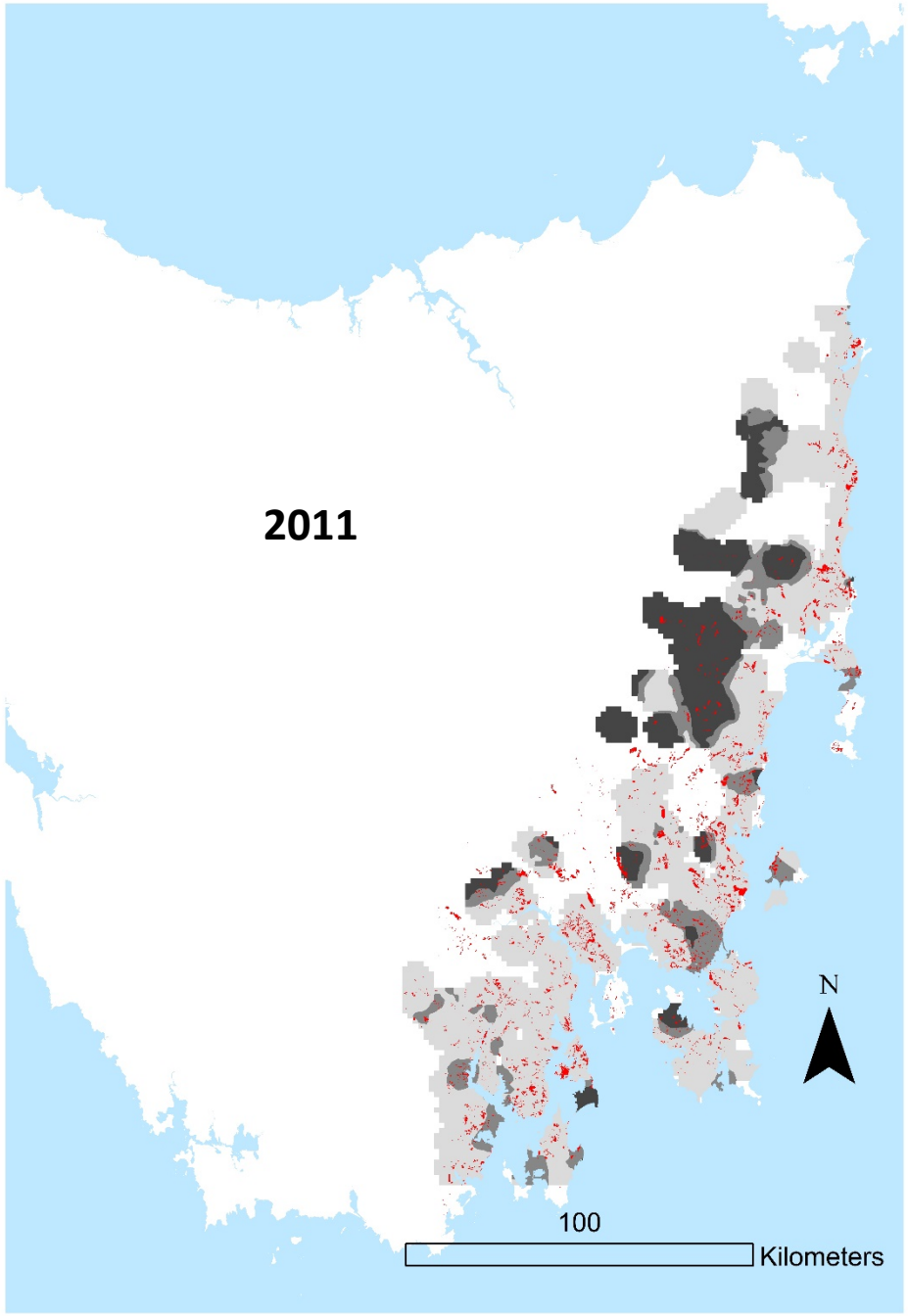
Appendix A

Figure S1c. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

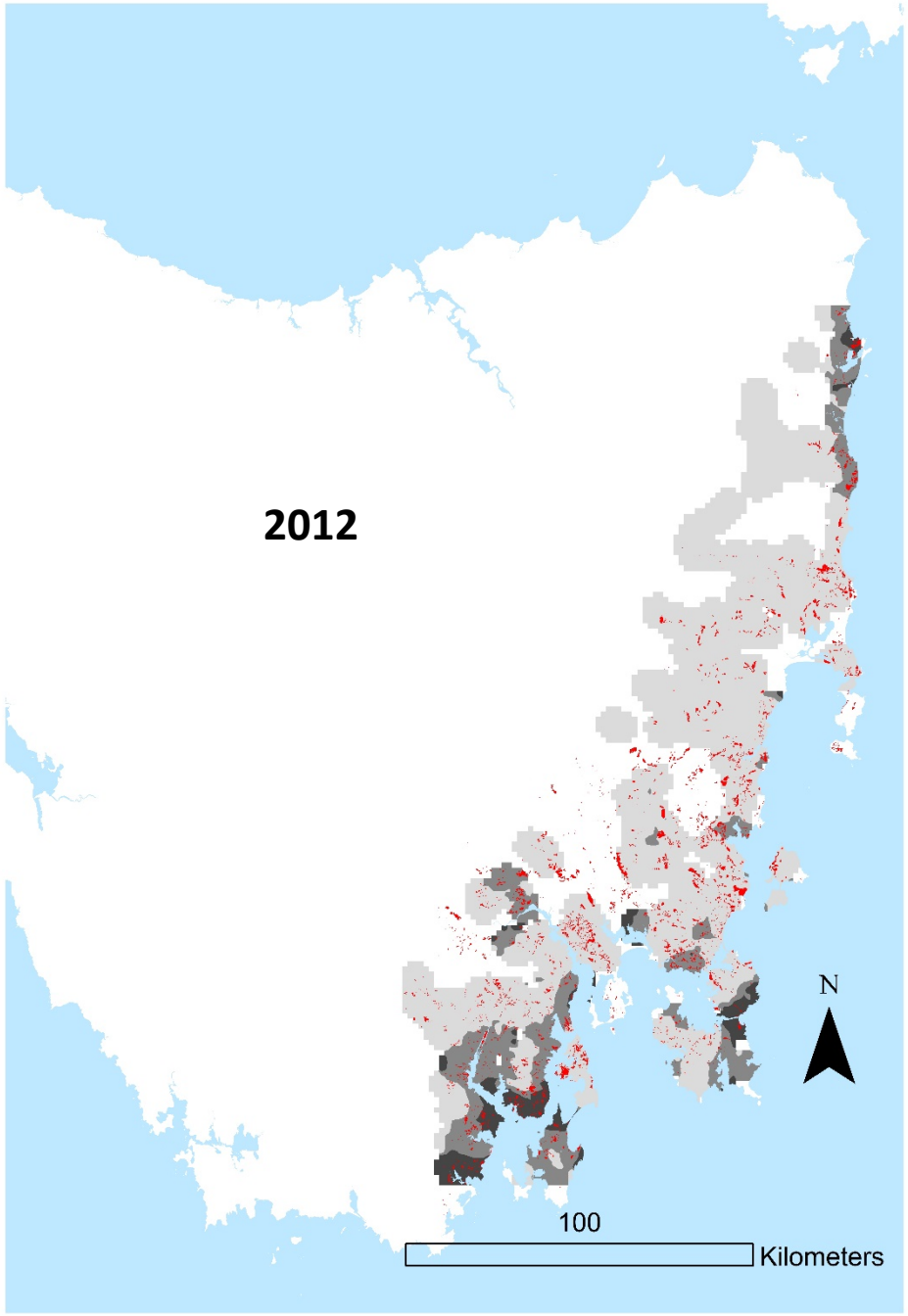
Appendix A

Figure S1d. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

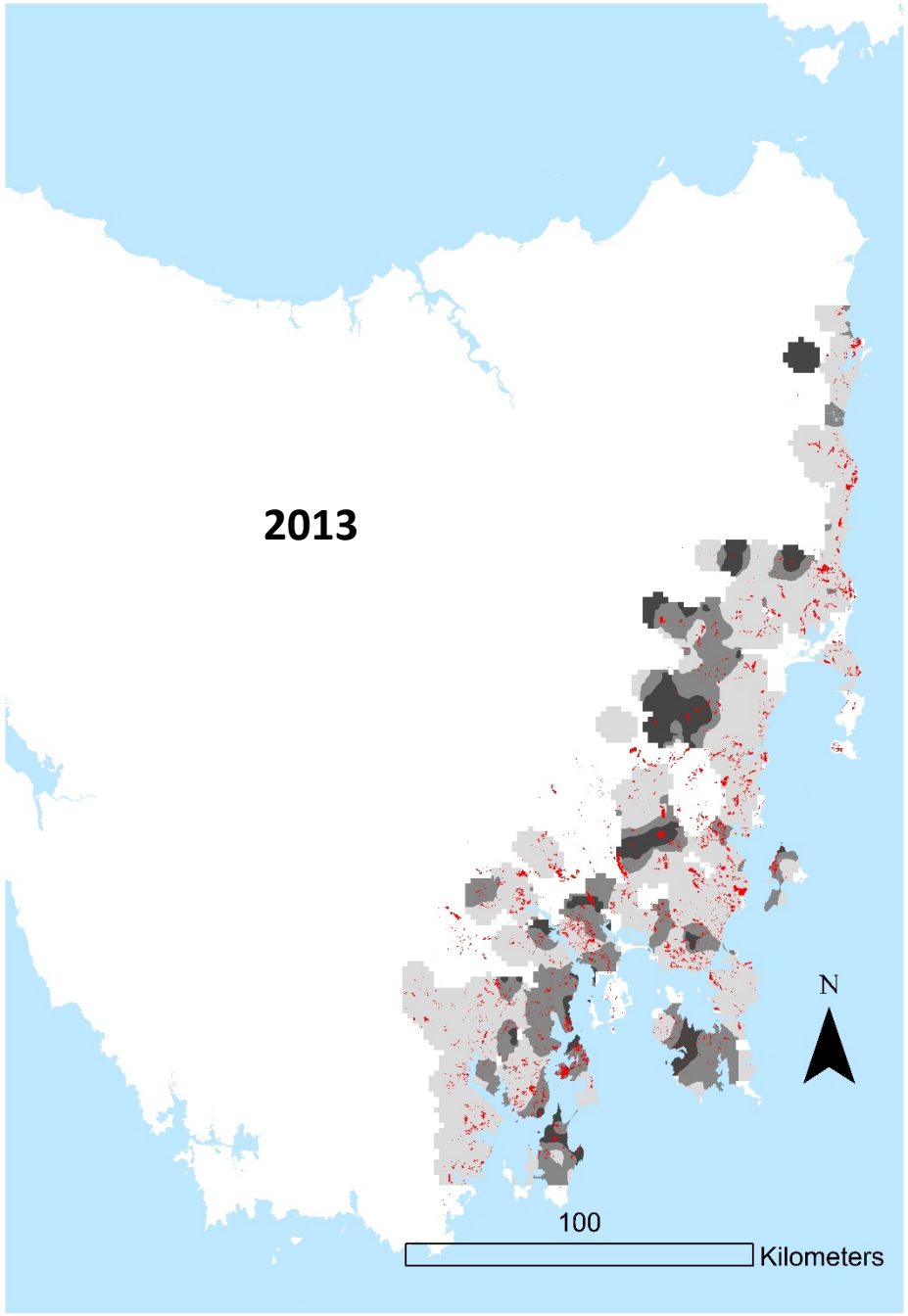
Appendix A

Figure S1e. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

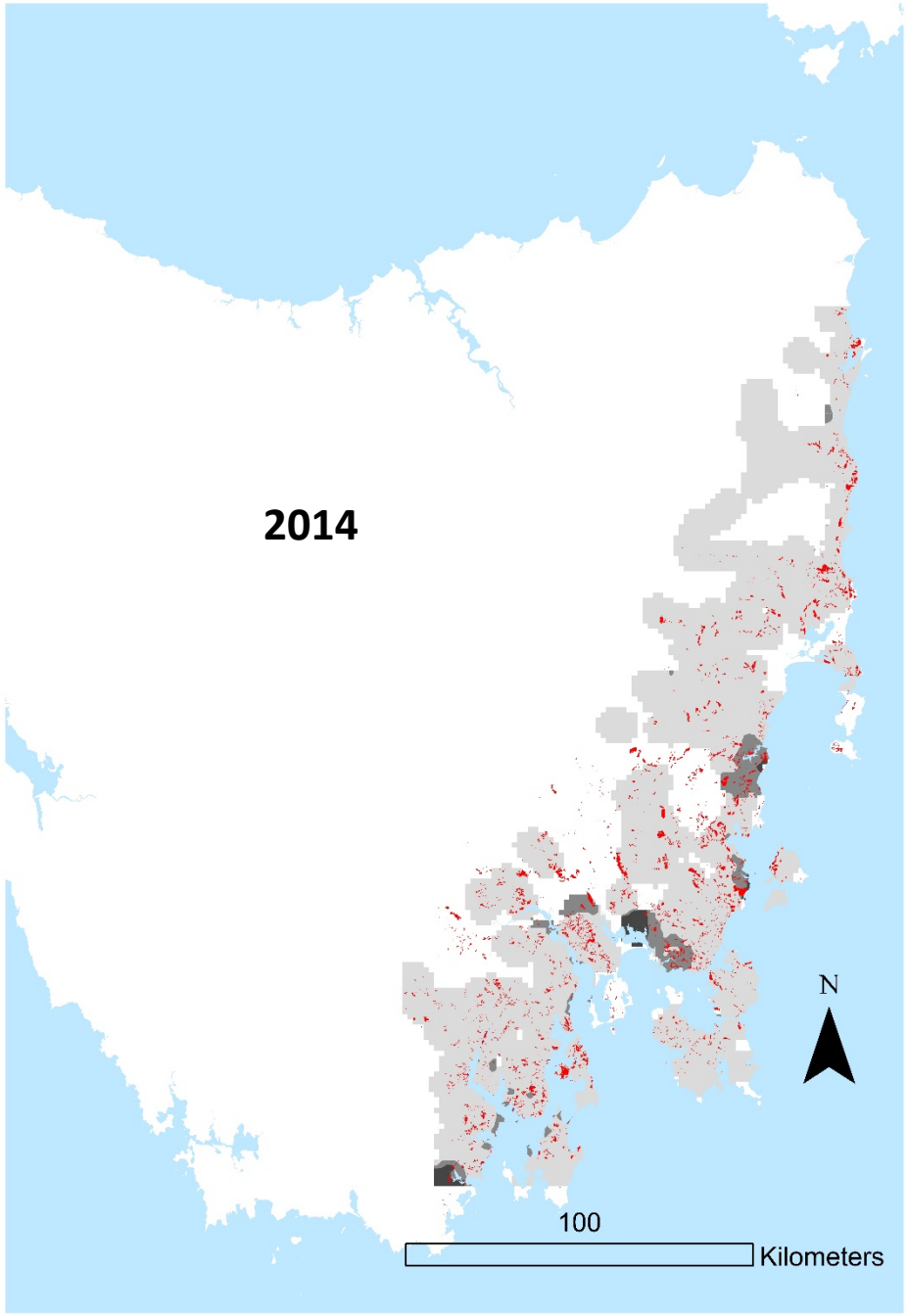
Appendix A

Figure S1f. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

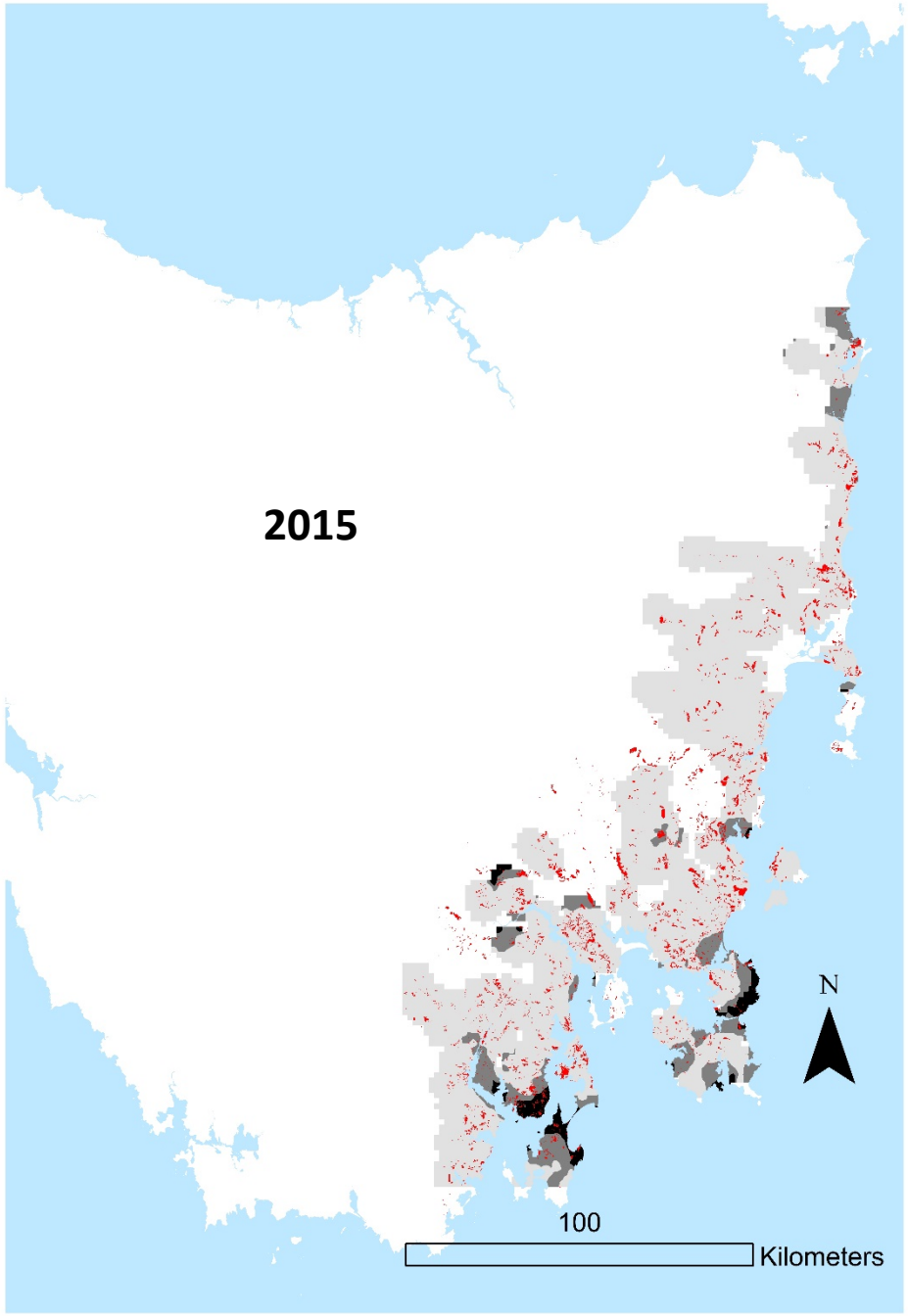
Appendix A

Figure S1g. Interpolated flowering conditions between 2009 and 2015 using kriging (cell size=1.5 x 1.5 km, search radius = 5 km)

Interpolated flowering intensity:

- light grey <1
- medium grey <2
- dark grey 2-4.

Red - mapped swift parrot foraging habitat (DPIPWE 2010).



REFERENCE

Department of Primary Industries Parks, Water and Environment (DPIPWE). (2010). GlobMap, The swift parrot foraging habitat map. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

Appendix B

Table S1. AIC scores for GAMs at the site and landscape-scales; 's' followed by parentheses indicates smoothed term; best model in bold text

	AIC scores	
Model	Site-scale	Landscape-scale
ABUNDANCE* ~ s(*OCCUPANCY*, by=*YEAR*) + *YEAR	**7341.9**	**39113.3**
ABUNDANCE ~ s(*OCCUPANCY*, by= *YEAR*)	7353.0	39299.8
ABUNDANCE ~ s(*OCCUPANCY*)	7453.9	41037.0
ABUNDANCE ~ *OCCUPANCY + YEAR*	7659.7	42449.1
ABUNDANCE ~ *OCCUPANCY*	7669.0	43098.7
ABUNDANCE ~ *YEAR*	9411.1	56609.3

Table S2. Significance of smoothed occupancy terms from the best site-scale GAM (Adjusted R^2 = 0.337, Deviance= 65%) and landscape-scale GAM (Adjusted R^2 = 0.497, Deviance= 64%).

	YEAR	EDF	χ^2	*p*
Site-scale	2009	3.787	242.7	<0.00001
	2010	3.790	264.2	<0.00001
	2011	4.875	238.8	<0.00001
	2012	4.361	286.5	<0.00001
	2013	4.913	235.2	<0.00001
	2014	8.543	330.3	<0.00001
	2015	7.558	330.8	<0.00001
Landscape-scale	2009	4.892	2211	<0.00001
	2010	8.783	1662	<0.00001
	2011	8.448	2122	<0.00001
	2012	7.950	2111	<0.00001
	2013	8.719	1065	<0.00001
	2014	8.610	2068	<0.00001
	2015	8.825	2376	<0.00001